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Personality and Well-Being in Felids: Assessment and Applications to Captive Management and Conservation

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Abstract

Research in animal personality has been increasing over the last decade, as scientists realise its importance to a variety of health outcomes. In particular, personality has been shown to have an effect on immune function, stress, infant survival, overall well-being, morbidity, and mortality. Because of this, personality can play an important role in captive management, especially as stress is often a problem for captive animals. Research has already shown that personality affects captive breeding efforts, enclosure grouping, and stress regulation in some species. Only a few studies have focused on felids, but these have shown that there are possible applications for personality in that taxon. Because most felids are endangered, and because many of them face special challenges in captivity due to their size and biology, this work aimed to increase knowledge on felids, using personality as a framework, with implications for captive management as a target. Focusing on five species, I assessed the personality of domestic cats, Scottish wildcats, clouded and snow leopards, and African lions, and the well-being of the four latter species. With the exception of the domestic cat, there has been little to no personality work in these species, and none on well-being. I then compared the data within and among these species. I found three main personality factors among the species, including dimensions I labelled Neuroticism, Dominance, and Impulsiveness, with some differences, including an Agreeableness factor in some species, and elements of Openness. As in other species, well-being was negatively related to Neuroticism in most of the study species. Taking into consideration each species' biology, natural history, and genetics, I discuss the implications and importance of using these species' personality and well-being assessments in both captive management and conservation efforts. The results indicate that, like in humans, a targeted, individual approach to care is the best use of personality for captive animals.

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This thesis is dedicated to Paul Johnson. Words can only poorly convey what his support means to me, how he went through this with me, the discussions that made this thesis what it is, his interest in what I do, and the sacrifices he has made.

Declaration

I am the author of this thesis and the work presented is my own. This work has not been submitted for any other degree or professional qualification.

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Chapter 1

Introduction

In the 1960s, Jane Goodall travelled to what is now Tanzania's Gombe National Park to study chimpanzees (*Pan troglodytes*). While there, she named the animals she was observing—including David Graybeard, the first animal observed to make and use tools, and the first to let her observe him—and attributed personalities (as well as minds, and feelings) to them (Goodall, 1986), using such words as affectionate and supportive. This type of personalisation had lost favour at the time in the scientific community, especially in ethology and psychology, and Goodall was often dismissed for it. More than five decades later, the dissent hasn't disappeared, but more scientists are inclined to admit that animals have personality, and there are numerous scientific publications on the subject, across a wide variety of species, from primates (Freeman & Gosling, 2010) to dogs (Jones & Gosling, 2005), cats (Feaver, Mendl, & Bateson, 1986), fish (Bell & Sih, 2007), and even some bugs (Watters & Meehan, 2007). It is no longer a question of whether non-human animals do or do not have personality, but how can we measure personality reliably? What are the similarities and differences in personality across species and taxa and what are the evolutionary implications? What relationships does personality have with other aspects of well-being, such as health and happiness? Finally, what can the results of such measurements tell us, and how can we use the results in everyday situations?

1.1 What is personality?

Personality, or a set of behaviours that remain consistent across context and time, is comprised of characteristics that describe these behaviours (Allport, 1937). Human personality research has a long history in psychology. While a detailed discussion of

this history is outside the scope of this work, a brief background in modern personality theory will provide the basis for understanding non-human animal personality research, and how it was formed.

Trait-based theories of personality originated with Allport (1937), who identified 4,500 traits to describe people; these traits occur in people as either cardinal (dominant), central (basic), or secondary (occasional) traits. By the 1970s, various trait-based personality theories had emerged (Cattell, Eber, & Tatsuoka, 1970; Eysenck & Eysenck, 1969). These were obtained by analysing ratings on traits using factor analysis to reveal personality factors as latent variables. Some posited 16 personality factors (with five secondary factors; Cattell et al., 1970), while others found three (Eysenck & Eysenck, 1976). These models evolved into the widely accepted Five-Factor Model (Costa & McCrae, 1992), and there are now decades of research completed on this model. This model is not set in stone (e.g., see Ashton et al., 2004; Chang, Connelly, & Geeza, 2012) and most research has been carried out in Western cultures (there has been some work done in other cultures, but it is not definitive: for example, see Church & Katigbak, 1989; McCrae et al., 1998; White, 1980; Yik & Bond, 1993). However, it is highly replicable (e.g., McCrae, Terracciano, & 78 Members of the Personality Profiles Cultures Project, 2005), and offers predictive value in terms of morbidity (e.g., Goodwin & Friedman, 2006), mortality (e.g., Booth-Kewley & Friedman, 1987), and well-being (e.g., Diener et al., 1999).

Although there were earlier iterations (Tupes & Christal, 1958), Goldberg first labelled the five-factor personality structure in humans the "Big Five" (1990), which included Extraversion/Surgency, Agreeableness, Conscientiousness, Emotional Stability vs. Neuroticism, and Culture; each of these broad domains are comprised of a variety of traits. However, little convergence among seemingly similar models led to further efforts to measure personality (John, Naumann & Soto, 2008). Costa and McCrae developed the NEO Personality Inventory (1985), which included Neuroticism, Extraversion, and Openness, and later the revised version,

which added facets of Agreeableness and Conscientiousness (1991). Neuroticism is comprised of facets including anxiety, angry hostility, depression, self-consciousness, impulsiveness, and vulnerability; Extraversion includes warmth, gregariousness, assertiveness, activity, excitement seeking, and positive emotions; Openness includes fantasy, aesthetics, feelings, actions, ideas, values; Agreeableness includes trust, straightforwardness, altruism, compliance, modesty, and tender-mindedness; and Conscientiousness includes competence, order, dutifulness, achievement striving, self-discipline, and deliberation (Costa & McCrae, 1992). Both sex and age effects have been shown for this model, with females rated higher in Neuroticism and Agreeableness than males, and some age-related decline in Neuroticism, Extraversion, and Openness and increase in Agreeableness and Conscientiousness (McCrae et al., 1999).

Personality in non-human animals

The modern origin of the idea that animals have personality goes back to Pavlov, who described four types of personality profiles (excitable, lively, quiet, and inhibited; Locurto, 2007) in dogs (*Canis familiaris*). His idea was that these personality types dictated how an animal would learn. According to Locurto (2007), these ideas influenced Eysenck's first model of human personality, which was built on a neurotic/emotionally stable, introverted/extraverted axis.

Early studies on non-human personality in the 1930s and 1940s (Crawford, 1938; Hebb, 1949; Yerkes, 1939) and 1970s (Buirski et al., 1973; Buirski, Plutchik, & Kellerman, 1978; Stevenson-Hinde & Zunz, 1978) were followed, in the 1990s to the present, with an array of studies on a variety of species, across disciplines.

Whatever advances Goodall made in getting scientists to admit that primates may have personality, the term itself is not used consistently because of the perceived notion that personality should only refer to humans (Gosling, 2008). Different terminology is used to describe personality or personality-like attributes

across fields like psychology, behavioural ecology, and veterinary studies. This makes it difficult to know if the same concepts are being discussed, and consistency in both terminology use (Weinstein, Capitanio, & Gosling, 2008) and measurement is needed. Across fields, three terms are generally used: temperament, behavioural type/syndrome, and personality.

Temperament is often described as an innate characteristic (Locurto, 2007), and is usually used with non-human animals and human infants (Jones & Gosling, 2005). However, the term is not used consistently.

Behavioural type and syndrome tend to be used in the field of behavioural ecology. Defined as a suite of correlated behaviours consistent across contexts among a population, a behavioural syndrome is related to a behavioural type, which is defined by correlated behaviours consistent across contexts in an individual (Sih, Bell, & Johnson, 2004). While these may be similar to personality and temperament, behavioural syndromes tend to be more one dimensional (purposefully: Weiss & Adams, 2013), measuring bold versus shy behaviour, or aggressive versus non-aggressive behaviour.

Finally, the term personality has been used to describe humans more commonly, although recently some scientists have begun to use it to refer to animals as well, as new studies have shown that anthropomorphism either doesn't affect some scientific results, or does not affect them negatively (Burghardt, 1991; de Waal, 2000, Kwan, Gosling, & John, 2008; Weiss et al., 2012; see Chapter 6) and that we are likely studying the same phenomenon. In fact, it has been recommended that we use the same term across species in order to ensure consistency (Gosling, 2008).

Regardless of what it's called, personality, or something like it, has now been measured in a large number of species, from orangutans (*Pongo pygmaeus, Pongo abelii*; Weiss, King, & Perkins, 2006), gorillas (*Gorilla gorilla*; Gold & Maple, 1994) and several species of monkeys (e.g., Weiss et al., 2011), canids (e.g., Fratkin et al., 2013; Macdonald, 1983; and see Jones & Gosling, 2005 for a review), and felids (Feaver et

al., 1986), to rodents, farm animals, horses, birds, fish, ants, butterflies, and cephalopods (see Gosling, 2001 for a review of many of the species studied). However, personality used in a psychological sense—that is, a set of characteristics that describe one's personality—has mainly been studied in primates.

Personality in primates

Stevenson-Hinde, Stillwell-Barnes and Zunz (1980) carried out what is now considered the seminal work on primate personality. They developed a questionnaire based on behavioural observations and applied it to rhesus macaques (*Macaca mulatta*). The authors found three personality factors: Confident, Excitable, and Sociable, as well as age, sex, and maternal effects. For instance, 2-3 year old females were more Excitable than males, and adult males were more Confident than adult females. Over the study's four years, Confident scores remained stable, while Excitable and Sociable were only stable in adults. For example, young males with an adverse experience within the first 8 months of life were more Excitable than other males, but just as Confident and/or Sociable. In terms of maternal effects, Confident and Sociable mothers had Confident and Sociable infants, respectively. Excitable mothers had infants that were not Confident. Finally, first-time mothers showed stability in their scores for Excitable from pre-pregnancy to post-pregnancy.

It wasn't until 1997, however, when King and Figueredo published their paper on chimpanzee personality and its similarity to the Big Five model of human personality, that the amount of personality research began to increase, and also to garner more attention. King and Figueredo used 43 traits from the Big-Five model to assess chimpanzee personality using Goldberg's (1990) taxonomy. Showing high reliability, the traits were factor analysed, with six resulting factors that they labelled Surgency, Dependability, Agreeableness, Emotionality, Openness, and Dominance. The first five are similar to the human Big Five, although with some differences in the traits that comprise them. For example, chimpanzee

Dependability was similar to human Conscientiousness, but did not include items related to trustworthiness and responsibility. Similarly, chimpanzee Openness did not have the same amount of traits in its composition as human Openness.

Age effects on chimpanzee personality include a positive relationship with Dominance (King, Weiss, & Farmer, 2005), Agreeableness, and Conscientiousness (King, Weiss, & Sisco, 2008), and a negative relationship with Extraversion, Emotionality, and Openness (King et al., 2005; King et al., 2008). Male chimpanzees are rated as more aggressive, emotional, and impulsive than females (King et al., 2008). In addition, chimpanzee Dominance and Neuroticism show evidence of genetic effects (Blatchley & Hopkins, 2010; Hong et al., 2011; Weiss, King, & Figueredo, 2000). King and Figueredo's (1997) work has been the basis for other research in chimpanzees (e.g., King et al., 2005; Weiss, King, & Hopkins, 2007; Weiss et al., 2009), orangutans (Weiss et al., 2006), and rhesus macaques (Weiss et al., 2011), using the same scale, which allows for comparisons among the results.

Orangutans have five factors of personality: Extraversion (similar to human and chimpanzee Extraversion, with the difference that traits related to sociality did not load highly in the orangutan, probably due to its semi-solitary status, as opposed to social humans and chimpanzees), Dominance (related to negative human Agreeableness and chimpanzee Dominance), Neuroticism (similar to both human and chimpanzee Neuroticism), Agreeableness (virtually identical to chimpanzee Agreeableness), and Intellect (neither a factor in chimpanzee or human personality, but comprised of such traits as decisive, disorganized, clumsy, intelligent, independent, and dependent/follower, elements of human Conscientiousness and Openness) (Adams, King, & Weiss, 2012; Weiss et al., 2006). All five orangutan personality factors have been shown to be heritable (Adams et al., 2012). No sex or age effects have been reported.

There has been more work done with rhesus macaques (e.g., Capitanio, 1999; Capitanio & Widaman, 2005; Stevenson-Hinde et al., 1980), but only one study using the same scale (Weiss et al., 2011). The latter found six factors of personality: Confidence (with similar traits included in human Neuroticism and Conscientiousness; positively correlated with chimpanzee and orangutan Dominance, orangutan Intellect, and negatively with chimpanzee and orangutan Neuroticism); Openness (including traits related to human Openness and low Conscientiousness, and closely related to chimpanzee Openness); Dominance (including traits related to low human Agreeableness, low Conscientiousness, and high Neuroticism; closely related to chimpanzee and orangutan Dominance); Friendliness (related to human Extraversion, Agreeableness, Conscientiousness, and Openness; similar to Extraversion and Agreeableness in chimpanzees and orangutans); Activity (related to low human Extraversion and Openness; similar to orangutan Extraversion), and Anxiety (related to human Neuroticism and low Conscientiousness; similar to chimpanzee and orangutan Neuroticism and low chimpanzee Conscientiousness).

Personality in felids

Regardless of the increase in personality literature, there is a bias toward studying species more closely related to, or more useful to humans. Among mammals, this has led to a large literature on personality in non-human primates (210 articles) (Freeman & Gosling, 2010). There is also a growing literature on dog personality (51 articles) (Jones & Gosling, 2005). By comparison, there are only 20 articles on personality in cat species.

By far, the most studied cat species, in terms of personality, is the domestic cat (*Felis silvestris catus*), with 85 percent of studies on felids focused on that species (see Chapter 3). An early study (Feaver et al., 1986) used a similar method to early primate work to assess personality in domestic cats. Using both behavioural

observations and a questionnaire based on Stevenson-Hinde et al.'s (1980) but altered to suit cat behaviour, the authors found three personality factors: Alert, Sociable, and Equable (as all the cats were female, sex effects were not investigated).

Other species studied include snow leopards (*Panthera uncia*; Gartner & Powell, 2012), cheetahs (*Acinonyx jubatus*; Wielebnowski, 1999), clouded leopards (*Neofelis nebulosa*; Wielebnowski et al., 2002), and tigers (*Panthera tigris tigris*; Phillips & Peck, 2007); however, there has only been one published article on each of these species.

The implications for felid personality research are far reaching. Approximately 59 percent of cat species are endangered or in decline, and their survival may depend on their success in zoos. However, because cat species naturally have large ranges, they often face challenges in zoo enclosures (Clubb & Mason, 2003). In small cages in shelters and laboratories, felid welfare is often compromised as well. While various techniques have been used to increase welfare, some species still face challenges in captivity. Knowing an animal's personality has the potential to help to address some of these issues. For example, Wielebnowski (1999) suggests that cheetahs rated highly on the dimension Tense-Fearful might have more difficulty in coping with the captive environment, and might therefore need more secluded enclosures and/or more hiding places.

In addition to using personality to address issues of welfare, it can also be used to address overall well-being and physical health, as it has been shown to be associated with these factors in humans (Deary, Weiss, & Batty, 2010), chimpanzees (King & Landau, 2003), orangutans (Weiss et al., 2006), gorillas (Weiss et al., 2013), and rhesus macaques (Weiss et al., 2011), and can play a role in conservation efforts (Carlstead, Mellen, & Kleiman, 1999; Powell et al., 2008) and other elements of captive animal management (Watters & Powell, 2012). In terms of both welfare and conservation, then, personality has the potential to play an important role that is, at the moment, underutilized. These ideas will be discussed further in Chapter 7.

1.2 Subjective well-being in non-human animals

A recent trend closely tied to animal personality research is the study of subjective[1] well-being, or happiness. This area has its origins in research on humans that has shown that well-being is tied to personality and, in turn, is associated with positive life events (Lyubomirsky, King, & Diener, 2005) and health (Diener & Chan, 2011). Subjective well-being is comprised of emotional responses, domain satisfactions (such as work, family, leisure, health, finances, self, and group), and global judgements of life satisfaction (Diener et al., 1999). In humans, external life circumstances do not play a strong role in long-term well-being (Lykken & Tellegen, 1996), with effect sizes ranging from .03 for age, .04 for sex, and .08 for marital status to .11 for occupational status, .14 for education, and .15 for social activity (DeNeve & Cooper, 1998); instead, most of its variance is due to personality, specifically Neuroticism and Extraversion (Costa & McCrae, 1980; Steel, Schmidt, & Shultz, 2008). This stems from the relationship between Neuroticism and negative affect and Extraversion and positive affect (Costa & McCrae, 1980).

Subjective well-being has been studied in humans since the 1950s, and a focus on the importance of positive emotions has been put forth since the 1990s as essential to good animal welfare, but measuring aspects of quality of life in non-human animals has proved challenging (Whitham & Wielebnowski, 2009). In their pioneering research on chimpanzees, King and Landau (2003) showed that subjective well-being can be reliably assessed in chimpanzees in a similar way as how it is assessed in humans. Using a scale based on human well-being measures,

[1] The word subjective refers to the measurement of an animal's experience, including the balance of positive and negative affect, and the perceived amount of control over important events (King & Landau, 2003).

Table 1 Subjective well-being questionnaire (King & Landau, 2003). The first two items were meant to be comparable to human scales of positive and negative affect, and the third to human scales of perceived personal control.

Estimate the amount of time each of the chimpanzees in your zoo is happy, contented, enjoying itself or otherwise in a positive mood. Assume that at other times the chimpanzees are unhappy, bored, freighted or otherwise in a negative mood.
Estimate, for each chimpanzee in your zoo, the extent to which social interactions with other chimpanzees are satisfying, enjoyable experiences as opposed to being sources of fright, distress, frustration or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience.
Estimate, for each chimpanzee in your zoo, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired social interactions, achieving a desired dominance status, and having access to desirable locations, devices, or materials in the enclosure.
Imagine how happy you would be if you were this chimpanzee for a week. You would be exactly like that chimpanzee. You would behave the same way as that chimpanzee, would perceive the world the same way as that chimpanzee, and would feel things the same way as that chimpanzee.

they asked caretakers to rate chimpanzees on four items (Table 1). They found a single latent variable across these four measures of chimpanzee well-being. This variable is positively associated with Dominance, Extraversion, and Dependability (later labelled as Conscientiousness). All six chimpanzee personality factors account for 52% of the variance in chimpanzee subjective well-being. Weiss et al. (2009) found that chimpanzee well-being negatively correlates with Neuroticism and positively with Dominance, Extraversion, Agreeableness, and Openness. In orangutans, Extraversion, Agreeableness, and (low) Neuroticism are related to subjective well-being (Weiss et al., 2006). Also, orangutan well-being is related to mortality, with animals rating higher on subjective well-being living approximately 11 years longer that orangutans who scored lower on the scale (Weiss, Adams, & King, 2011). Finally, in rhesus macaques, subjective well-being is positively related to Confidence and Friendliness, and negatively related to Anxiety (Weiss et al., 2011). In addition, chimpanzee subjective well-being is heritable, and genetically correlated with Dominance (Weiss, King, & Enns, 2002); orangutan subjective well-being is also heritable (Adams et al., 2012).

Taken together, personality and well-being assessment could be very important for outcomes in endangered cat species living in captivity, as well as domestic cats in shelters, as personality, and therefore well-being, has been shown to affect captive breeding (e.g., Wielebnowksi, 1999), immune function (e.g., Capitanio et al., 2008), stress levels (e.g., Wielebnowski et al., 2002), and other health outcomes including mortality (e.g., Weiss et al., 2013) and morbidity (e.g., Natoli et al., 2005). Similarly, it has the potential to affect management decisions, including enclosure grouping (Stoinski et al., 2004), targeted enrichment (Powell & Gartner, 2011), and breeding success (e.g., Wielebnowski, 1999), as well as conservation measures such as reintroduction (e.g., Bremner-Harrisonet al., 2004) and translocation (e.g., Shier & Swaisgood, 2009).

This work therefore assessed the personality of five species in the felid taxon—domestic cats, Scottish wildcats, clouded and snow leopards, and African lions (*Panthera leo*)—and the well-being of the four latter species. The aims were to assess whether personality and subjective well-being could be reliably measured in these species, to provide a personality structure for each species, and to see if personality was related to well-being in any of these species. In addition, the five personality structures were compared to assess if there were any similarities, what the differences were, and if a possible evolutionary path could be seen, as the species covered both genetic lines of felids (Pantherinae and Felinae), and the first and last species to evolve in the modern living taxon. In addition, I wanted to see if an overall taxon personality structure could be reliably and sensibly formed based on these five species. Finally the results were put into a framework that describes personality as a tool for use in captive situations—in this case zoos and shelters. Therefore implications and possible applications of the results are discussed.

Chapter 2

Felidae—Natural history and biology

To understand the "whole animal" (Wemelsfelder et al., 2001), it is necessary to look at every aspect of its life, including its physical characteristics. While differences among species, and even subfamilies, exist in Felidae, the similarities are sizeable. These parallels exist across the species' biology (including morphology and diet), ecology, and, of course, genetics. This chapter highlights the similarities and differences among the study species, which will offer a biological basis for understanding the results, including age and sex effects on personality and well-being, as well as the similarities among personality factors. In addition, information on threats to existence that each species faces elucidates the need for conservation and welfare efforts, as discussed in Chapter 7. The phylogenetic relationship in this family can be seen in Figure 1, which shows Bayesian analyses and two independent iterations of bootstrapping estimates to illustrate the phylogenetic reconstruction of Felidae carried out by Wei et al. (2011). The authors estimated bootstrap values using 1,000 nonparametric bootstraps and 50 random addition sequence replicates; bootstrap values had to be >70% to be supported.

2.1 Subfamily Felinae

The Scottish wildcat (*Felis silvestris grampia*)

The Scottish wildcat is a subspecies of the European wildcat (*Felis silvestris*; Beaumont et al., 2001). The European wildcat was the second to speciate from the subfamily Felinae, after the sand cat (*Felis margarita*) and before the Southern African wildcat (*Felis silvestris cafra*; Figure 2; but see also Johnson et al., 2006). At present, there are an estimated 35-400 Scottish wildcats left in the wild ("Scottish Wildcat Association," n.d.-e; Davis & Gray, 2010; Macdonald et al., 2004;

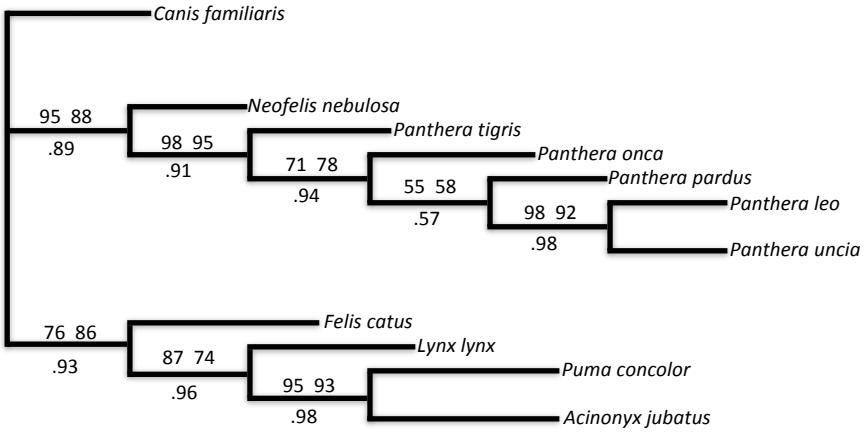

Figure 1 Phylogenetic relationships based on analyses of combined 12S rRNA+16S rRNA+ND2+ATP8+ND4+ND5+Cyt *b*. Maximum likelihood, maximum parsimony, and Bayesian analyses obtained similar tree topologies. Bootstrap values are above the branches; Bayesian probabilities are below the branches. *Recreated from Wei et al., 2011, with kind permission from Springer Science and Business Media (Figure 3, © the Authors)*

Yamaguchi et al., 2004). While the European wildcat is the most common and widely distributed wild cat, and is labelled Least Concern by the IUCN Red List, there are certain subspecies, of which the Scottish wildcat is one, whose numbers suggest an IUCN classification of Critically Endangered (Driscoll & Nowell, 2010), mainly due to hybridisation.

Biology

The Scottish wildcat is a small cat, with males weighing on average 4.9kg and females 4.2kg (Balharry & Daniels, 1998). They can live to approximately 10 years old in the wild (Balharry & Daniels, 1998). They have a thick coat of medium-length fur, with a bushy tail. The skin is greyish brown with black markings (Taylor, 1946). A solitary species, they are mainly nocturnal, and make use of dens such as hollow trees or rabbit burrows (Macdonald & Barrett, 1993). They tend to avoid areas of human habitation.

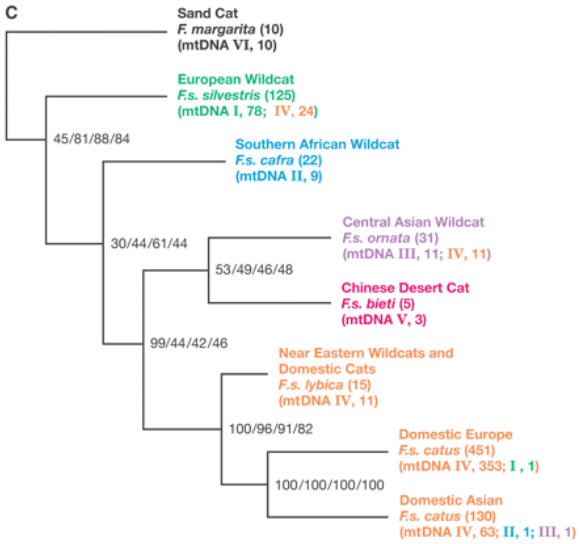

Figure 2 Phylogenetic relationships among F. silvestris groups as defined by composite short tandem repeat (STR) genotypes based on 36 STR loci. Tree is rooted at sand cat. Bootstrap values at corresponding nodes are based on 1000 iterations with the following measures (from left to right): Dps=1 − (ps)/Dkf =1 − (kf)/Dps=−ln(ps)/Dkf=−ln(kf). All methods resulted in identical topologies. Individuals were clustered into representative populations based on STRUCTURE Q-value of 0.80 or greater with the same loci. All known domestic cats cluster into domestic-Asia, domestic-Europe, or Near Eastern wildcats, regardless of provenance, and these groups also cluster together. From Driscoll et al., *Science,* 27 July 2007: vol. 317 no. 5837, 519-523. Reprinted with permission from AAAS.

Diet

The Scottish wildcat diet is comprised of 70% small mammals (voles, mice, and shrews), with lagomorphs the most important prey. A variety of bird species comprise 20% of their diet; 17% of which are game birds (Balharry & Daniels, 1998). The latter is important in light of conservation efforts, as some land managers in Scotland target domestic cats as pests, and may mistake wildcats for them.

Reproduction

Although evidence of oestrus is found in all seasons, wildcats seem to mate most often in the spring (Daniels et al., 2002; Goodrowe et al., 1989). The mean litter size is 4.3 (range=3-6) (Daniels et al., 2002). As in many cat species, only the mother cares for the kits, for approximately five months. Males become sexually mature after one year, females after nine months (Scottish Wildlife Trust Policy, 2011).

Morphology

In attempting to distinguish them from domestic cats, much work has been done on Scottish wildcat intestine and limb size, pelage identification, and skull differentiation (Daniels et al., 1998; French et al., 1988; Kitchener et al., 2005; Reig et al., 2001; Yamaguchi et al., 2004). Daniels et al. (1998) found two distinct groups when assessing intestine and limb length. Group 1 (wildcat, or hybrid) had shorter intestines and longer limb bones than Group 2 (domestic cat). In addition, the relationship between intestine and limb bone length was different in the two groups, therefore suggesting two populations. In the same study, neither pelage nor skull size revealed distinct populations when analysed alone. However, when analysed with other variables, differences were found. Group 1 cats had larger mean skull size, and more stripes on the body, legs, and tail.

French et al. (1988) analysed skull size in Scottish wildcats and domestic cats. They found that recent (those collected between 1953 and 1963) and modern (1975-1978) wildcats were different from those collected earlier (old: 1901-1941), which they attributed to hybridisation. They found that all wildcat groups could be clearly distinguished from domestic cats—with wildcats having larger, more robust skulls, especially the neck, cranium, and jaw—but that most likely the modern and recent groups represented hybrids.

Reig et al. (2001) had similar results using three-dimensional morphometrics, finding wildcats had larger skulls, the lowest braincase capacity index, and the greatest sexual dimorphism. Male wildcat skull sizes were 7.2% larger than domestic cats', and females 3.8% larger. Following Schauenberg's braincase capacity index (1969) (the ratio of braincase capacity to total length of the skull), they found that wildcat skulls had the lowest values, but variation was always larger in females, for both groups.

Yamaguchi et al. (2004) also looked at skull differentiation, which is measured using the cranial index (CI), a ratio of skull length to cranial volume; CIs

of more than 2.75 represent smaller cranial capacity, which is associated with domesticated animals (Kilshaw et al., 2010). They found significant differences between wildcats and non-wildcats on a cluster analysis of five skull character scores and a total skull score, with four distinct groups: domestic cats (CI= 3.18), hybrid cats (CI=2.53), and two groups of wildcats (CI=2.28; 2.37). These results were in line with museum classification systems, and the authors suggest that skull character scores and pelage are important features in classification.

Finally, Kitchener et al. (2005) looked at pelage and skull size. They were able to differentiate three main groups: wildcats, hybrids, and domestic cats. Width of brain case, postorbital constriction, distance between infraorbital foramina, cranial volume, and cranial index were statistically different between domestic cats and wildcats combined with the hybrids. Pelage characteristics traditionally considered to define the Scottish wildcat (Figure 3) were found to be similar to differentiation among skull sizes, distinguishing three groups. Wildcats had scores of greater than two for all seven characteristics that were the most highly significant for differences among the groups (extent of dorsal line, shape of tail tip, distinctness of tail bands, broken stripes on flanks and hindquarter, spots on flanks and hindquarters, stripes on nape, and stripes on shoulder). Wildcats also always scored 3 on stripes on nape and shoulder. All domestic cats and some hybrids had a score of 1 for any of the seven characteristics. Domestic cats were characterized by white coloured chins, stripes on cheeks, dark spots on underside, white on flank, white on back, colour of tail tip, stripes on hind leg, and colour of the back of the ear.

These studies show that there are clear differences among Scottish wildcats, hybrids, and domestic cats. Presently, a genetic test is being developed by the Royal Zoological Society of Scotland, but is not completed as of yet. The aim is to identify which regions of the wildcat genome differ from those of the domestic cat, to aid in identification of pure-bred cats (see section below on Genetics).

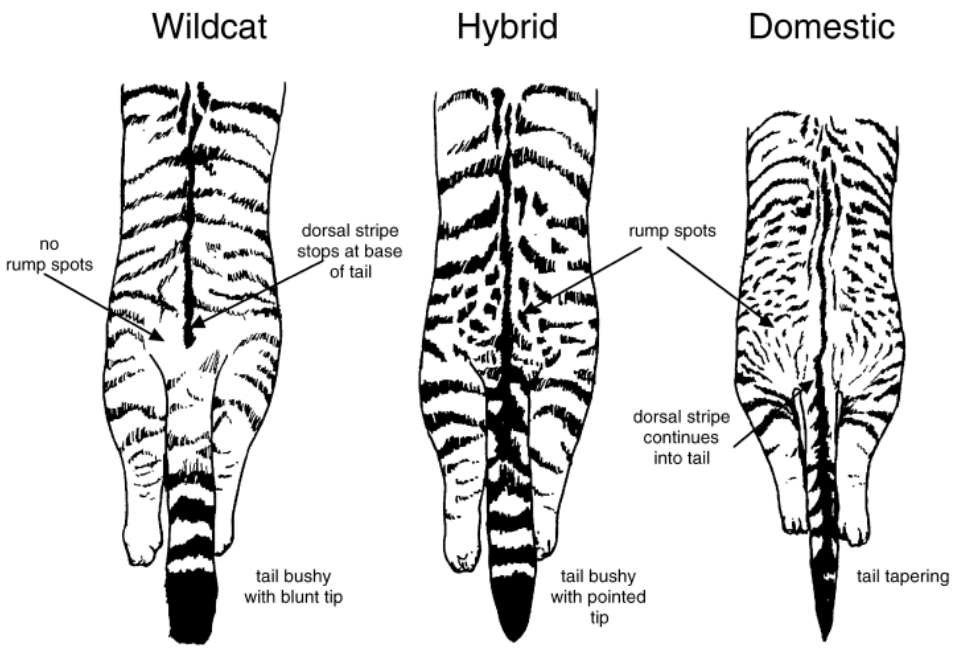

Figure 3 Pelage characteristics used to differentiate Scottish wildcats from hybrids and domestic tabby cats (reproduced with permission from Beaumont et al., 2001).

Natural history

The Scottish wildcat is the descendent of the European wildcat. The latter was isolated on the British Isles after the last Ice Age, around 7,000-9,000 years ago (wildcat skeletal evidence has been found in British caves [Yalden, 1982]), and became a distinct sub-species.

Before 1800, the Scottish wildcat was found throughout mainland Britain. By 1862, due to hunting and habitat loss, it had disappeared from England and Wales. At the end of the 19th century, it was scarce in Scotland as well (Langley & Yalden, 1977); this was probably due to persecution by gamekeepers, who targeted the wildcat for predation on game birds. However, numbers began to increase when forests began to be planted in the central Highlands of Scotland during World War I, providing critical habitat (Scottish Wildlife Trust Policy, 2011). A survey in the 1980s suggested that the wildcat was present in the north of Scotland (Easterbee et al., 1991), but another in 1998 claimed that they were limited to the northeast

(Balharry & Daniels, 1998); more recent work has shown them to be in the northwest as well (Davis & Gray, 2010).

Ecology

Scottish wildcats are isolated to Scotland, mainly in Aberdeenshire, Caithness, Sutherland, the Ardnamurchan Peninsula, and Morven (with sightings in Perthshire, the Cairngorms, and the Central Highlands) (Davis & Gray, 2010). Forests are critical to wildcat territory (Klar et al., 2008), and Scottish wildcats prefer mixed areas of woods and scrub (for shelter), and moors or grassland (for hunting) (Scottish Wildlife Trust Policy, 2011). Territories range from 500 ha for males and 180 ha for females, depending on prey availability. Same sex animals do not have overlapping territories, but males may have several females within their territory.

Threats

Presently, the main threats to the Scottish wildcat population include introgression with domestic cats, habitat loss, persecution, and disease transmission from domestic cats (Scottish Wildlife Trust Policy, 2011).

Introgression

Domestic cats were introduced to Britain by the Romans 2,000 years ago (Kilshaw et al., 2010). Therefore, the potential for interbreeding has existed for the same amount of time (Daniels et al., 2001; but see Kitchener, 1998). In recent genetic studies, although distinct wildcat and domestic cat groups have been found, the wildcat group is not clearly a distinct species, but more likely a hybrid (see Genetics section).

Habitat Loss

Although Scotland has been deforested for some time, starting in approximately 6000 BP[2] with an increase of deforestation around 2500-2000 BP and again during the Middle Ages due to agriculture (Newton, Stirling, & Crowell, 2001), some suggest that habitat loss in the form of current land development may contribute to species decline in the Scottish wildcat (Scottish Wildlife Trust, 2011). This decline since the Middle Ages, coupled with an expansion in range as a result of newly planted woodland in the early 1900s (Beaumont et al., 2001), supports this argument. In addition, because wildcats prefer a mix of various types of environments, habitat fragmentation may still present a problem (Silva et al., 2013).

Persecution/misidentification

Scottish wildcats are fully protected under Schedule 5 of the Wildlife and Countryside Act 1981, and are listed on Annex IV of the European Union Habitat Directive (and are therefore protected in the United Kingdom under Schedule 2 of the Conservation Regulations). However, they are still shot on sporting estates, where feral cats are legally shot as a control measure (Scottish Wildlife Trust Policy, 2011). Whether this is due to misidentification or on purpose is unknown.

Disease

Domestic cats can transmit disease to Scottish wildcats, including feline leukaemia virus (FeLV), feline coronavirus, feline calicivirus, feline herpesvirus, and feline foamy virus. FeLV is the most serious of these diseases, and may cause fatality in the wildcat (Daniels et al., 1999). Interestingly, there has been no feline

[2] BP is an archeological term meaning "before present", and defines the present as 1 January 1950 (Council of Biology Editors, 1994). Therefore, the calculated date is, in this example, 6000 years before 1950.

immunodeficiency virus found in Scottish wildcats, although there is an estimated 57% of the population of feral cats with the disease (Daniels et al., 1999).

Genetics

Hubbard et al. (1992) found two distinct groups of cats by looking at gene frequencies in their sample (χ^2=9.14, p<.001). In addition to wildcats and domestic cats, the authors found a large amount of hybrids.

Beaumont et al. (2001) looked at genetic diversity in Scottish wildcats and domestic cats using nine microsatellite loci. They found allele frequency differences between the two species, with two alleles found in wildcats that were not present in domestic cats. They concluded from their study that it is unlikely that a pure wildcat—as it was when it first became a subspecies after Britain became an island—still exists, but that two distinct subspecies are present: domestic cats and wildcats that are genetically distinct but that still shows signs of introgression.

Kilshaw et al. (2010) looked at previous data, in order to compare genetic with morphological data. They found that most of the wildcats used in research on pelage and other morphological characteristics have been either hybrids or domestic cats. However, a small percentage (4.6%-13.1%) is correctly classified as wildcats, according to the comparative genetic study they ran, which identified three distinct groups of cats: wild, hybrid, and domestic. In addition, pelage assessment, according to both the "strict" and "relaxed" definitions by Kirchner et al. (2005), seems to be an accurate measurement, and matches the genetic classification (strict: χ^2=6.23, df=1, p=.029; relaxed: χ^2=6.79, df=1, p=.030; Kilshaw et al., 2010). In addition to pelage, cranial differentiation matches mtDNA: individuals with wildcat mtDNA had larger crania than those with domestic mtDNA (Kilshaw et al., 2010).

Kilshaw et al. (2010) also found one allele in domestic cats that is not in wildcats, therefore differentiating the two groups into distinct species. A significantly higher degree of sub-structuring between wildcats and domestic cats

was found, which indicates minimal gene flow between the two groups (hybrids fell in between) (Kilshaw et al., 2010). Two genetic clusters (wildcat/domestic cat) were found using Bayesian cluster analysis without any *a priori* information. When *a priori* information was incorporated into the model, 100% of wildcats as identified by the Strict ID and 76% of those identified by the Relaxed ID were in the wildcat genotype cluster. Seventy-three percent of those identified as domestic cats were in the domestic cat genotype cluster, with hybrids falling between.

The domestic cat (Felis silvestris catus)

Most closely related to the African wildcat (*Felis silvestris lybica*; Figure 2), the domestic cat is largely considered an invasive species, mainly because it has succeeded in a variety of climates and can be found on every continent except Antarctica. The worldwide population exceeds 500 million (Rochlitz, 2000). In the United States, Australia and Europe, there are an estimated 101.48 million pet cats, while in the United States and the United Kingdom there are approximately 42 million cats without homes (Rochlitz, 2000).

Biology

The weight of domestic cats ranges between 2kg and 5kg. Females weigh less than males on average, ranging from 3-4kg and males from 3-7kg. There are some breed differences as well, with American Ragdolls and Maine Coons weighing up to three times as much as the average, and Singapura weighing only 2-3kg (McCune, 2010).

Overall life expectancy ranges from nine to fourteen years, although many cats live into their twenties (McCune, 2010). Cats aren't functionally old—including cognitive and motor function—until at least their 16th year (Bradshaw, 1992).

Cats have long been thought to be solitary; however, as in other felids such as cheetahs, tigers and lynx (Kitchener, 2000), this has been shown to be variable, and dependent on food resources (Liberg et al., 2000).

Another assumption often made of cats is that they're either nocturnal or crepuscular. However, studies have shown that they experience behavioural and brain activity (Sterman et al., 1965) and spread feeding bouts throughout the day and night (Fitzgerald & Turner, 2000).

Diet

Cats are obligate carnivores. Their main prey is comprised of small mammals (rodents and rabbits), but they also will eat birds and lizards (Fitzgerald & Turner, 2000).

Reproduction

Domestic cats are induced ovulators. Females are sexually mature between seven and twelve months, and have a 63-day gestation period (Bateson, 2000). The average litter size is between three and six kittens (range 1-10; McCune, 2010).

Morphology

Selective breeding has resulted in many morphological modifications, including long-haired and short-haired breeds with different coloration (Bradshaw, 1992). Thirty-eight breeds have been genetically differentiated (Menotti-Raymond et al., 2012), and there is some evidence of differences in behaviour among breeds. For example, cats with the non-agouti allele (usually black cats) are more tolerant of crowding and the conditions of urban life (Todd, 1977). Red, cream, or tortoiseshell kittens struggle for a longer time and make more escape attempts when handled by an unfamiliar person than other coloured kittens (Ledger & O'Farrell, 1996). The orange allele may be linked to aggressiveness in males, while lacking the agouti allele is linked to greater amicability and aggregative tendencies (Robinson, 1977).

Natural history

There are varying ideas on whether cats domesticated themselves (Driscoll et al., 2007) by feeding on rodents in grain stores or were domesticated by humans as evidenced by wildcat remains from 6000 BCE found in Khirokitia on Cyprus, which was previously—presumably—wildcat free, therefore implying that humans brought the wildcat to the island (Serpell, 2000).

Ecology

Cats live in vastly differing climates, from forests to tundra (Global Invasive Species Database, 2011.) Home range sizes vary similarly, with females having a relatively small range in Jerusalem (.27-.29 ha), for example, but 170 ha in the Australian bush; males have ranges that are three times the size of females' (Liberg et al., 2000). This is probably related to amount of space, prey, and availability of mates.

Threats

One of the largest welfare issues for domestic cats is the number of abandoned, stray or feral cats/kittens (Rochlitz, 2000). These cats live without a known food source or shelter, are often exposed to harsh weather conditions, infection, or attacks by other animals. Many end up in shelters, where an estimated 71% in the United States alone are euthanised because they aren't adopted ("Animal Shelter Euthanasia," n.d.-a).

The reasons for this very high rate of euthanasia include failure to spay/neuter, irresponsible breeding, low adoption rates, and low shelter entrance rates (only an estimated 20% of new animals come from shelters; "Pet Overpopulation," n.d.-d). In addition, in the United States, 6-8 million pets are given up to shelters, for a variety of reasons, including having too many pets, allergies, moving, costs, housing issues, no homes for littermates, house soiling,

personal problems, inadequate facilities, and behavioural problems involving other pets (Scarlett et al., 1999).

Genetics

There are eight phylogenetic lineages of felids (ocelot lineage, pantherine lineage, caracal group, puma group, Asian leopard cat group, baycat group, lynx genus, and domestic cat lineage; Serpell, 2000). The domestic cat and the African wildcat probably diverged from a common ancestor approximately 131,000 years ago (Driscoll et al., 2007). Recent genomic assessment suggests that cats were domesticated in the Near East (Israel, Saudi Arabia, Bahrain, and the United Arab Emirates), with five founders across the region (Driscoll et al., 2007).

2.2 Subfamily Pantherinae

The clouded leopard (*Neofelis nebulosa, Neofelis diardi*)

The first species to branch off from Carnivora in the Felinae family and recently identified as possibly part of the Pantherinae subfamily, the clouded leopard has recently been separated into two species, *Neofelis nebulosa*, and *Neofelis diardi* (Kitchener, Beaumont, & Richardson, 2006; Wilting et al., 2007). The former lives in mainland Southeast Asia, while the latter lives in Sumatra and Borneo.

Listed as Vulnerable on the IUCN Red List, with a decreasing population, both species of clouded leopard, rarely seen in the wild, are difficult to assess in terms of population size. There have been some regional studies (e.g., Grassman et al., 2005), but no overall numbers are available.

Biology

Clouded leopards are medium-sized cats, weighing between 11-20kg (Nowell & Jackson, 1996). They are specialized climbers who also swim. On average they live

11 years, but have been known to live up to 17 (Nowell & Jackson, 1996). *N. nebulosa* is nocturnal, but it is suggested that *N. diardi* may be less so (and more crepuscular), due to a lack of predators on Borneo (Rabinowitz, Andau, & Chai, 1987). Like much of its behaviour in the wild, whether it is solitary or semi-solitary is unknown.

Diet

Clouded leopards are thought to eat relatively large ungulates, including deer and wild boar, but also primates, birds, and small mammals (Nowell & Jackson, 1996).

Reproduction

Gestation is approximately three months, with one to five cubs being born (usually three; Nowell & Jackson, 1996). Clouded leopards are sexually mature at 26 months. Clouded leopards are known to be one of the hardest cats to breed in captivity, with males being particularly aggressive to females, high cub mortality, and self-injuring behaviours common (Wielebnowski et al., 2002). Introducing potential mates at young ages (between four and six months old) has increased breeding success; however, with only 277 clouded leopards in captivity (and only 69 in the Association of Zoos and Aquariums' Clouded Leopard Species Survival Plan program, "Clouded Leopard Locator," n.d.-b), most of whom are adults, this method is difficult.

Morphology

Clouded leopards are named for the pattern on their yellow to brown fur, which is marked by circular black "clouds" of colour. The tail is as long as their head to body length (up to 80-90cm), and they have short legs and the longest canines of any felid, relative to body size (Nowell & Jackson, 1996).

Natural history

Clouded leopards were the first species of the Panthera line to evolve, 8.66 million years ago (Wei et al., 2011, who suggest that the species be included in this genus). There is very little known about the species in the wild, as they are elusive, arboreal, and live in forests that make observation impractical (Nowell & Jackson, 1996).

Ecology

Clouded leopards live in Nepal, India, Bhutan, Bangladesh, Myanmar, China, Vietnam, Cambodia, Laos, Thailand, Malaysia, and Indonesia, specifically Borneo and Sumatra; they are now extinct in Taiwan. They prefer tropical rainforests, but have also been seen in deciduous forests. While their range is not known in general, two studies (Austin et al., 2007, in Grassman et al., 2005; Grassman et al., 2005) in Thailand have shown that females and males maintain 30-40km^2 ranges, with an inner core of 3-5km^2 (Grassman et al., 2005), and that there is overlap in territories.

Threats

Deforestation

Southeast Asia is undergoing the world's fastest rate of deforestation (Nowell & Jackson, 1996). Because clouded leopards' preferred habitat is closed forest, this is the biggest threat facing this species. However, it is unknown how adaptable the animals may be (Rabinowitz et al., 1987). Because there is evidence of populations in both logged areas and also grassland, scrub, and mangrove swamps (Nowell & Jackson, 1996), it is possible that they may be able to adapt to a changed landscape.

Illegal trade

Clouded leopards are hunted mostly for their teeth and their pelts, which have been found being sold in southeastern China, Taiwan, Myanmar, Laos, Vietnam,

Cambodia, Nepal, and Thailand (Nowell & Jackson, 1996). They are also hunted for their bones to be used in traditional Asian medicine, meat sold in Thailand and China, and for the pet trade.

Genetics

Although clouded leopards were thought to be a separate genus than other Panthera felids, recent genetic work has shown that they belong to that lineage (Janczewski et al., 1995; Johnson & O'Brien, 1997; Yu et al., 2004; King et al., 2007; O'Brien & Johnson, 2007; and Wei et al., 2011).

The snow leopard (*Panthera uncia*)

Along with the African lion, the snow leopard was the last to speciate in the Pantherinae subfamily. Currently, there is an estimated four to six thousand snow leopards left in the wild (McCarthy & Chapron, 2003), however the number of animals that breed successfully is estimated at about half that number (Nowell, Schipper, & Hoffmann, 2007). In the last decade, the number is thought to have decreased (Theile, 2003), and there is no firm population count. The snow leopard is labelled Endangered by the IUCN Red List, with a decreasing population trend.

Biology

The snow leopard is a medium-sized cat, typically weighing from 35-55kg (Nowell & Jackson, 1996). They have a distinctive tail, the length of which is 75-90% of their body length, which ranges from 100 to 130cm (Hemmer, 1972). In captivity, snow leopards have lived up to 21 years (Wharton & Freeman, 1988); it is unknown how long they live in the wild, but some estimate that they might not reach 10 years (Theile, 2003). Snow leopards are thought to be solitary, although maternal groups

of two to four animals have been known to form (Fox, 1989). They are crepuscular (Jackson, 1996), like many cat species.

Diet

Snow leopards' primary prey includes sheep and goats, most commonly blue sheep (*Pseudois nayaur*), Asiatic ibex (*Capra ibex sibirica*), markhor (*Capra falconeri*), and argali sheep (*Ovis ammon*), but they will also eat rodents and birds (Fox, 1989).

Reproduction

Snow leopards breed from January to March, and generally produce two to three cubs after approximately three month's gestation. The cubs are weaned at about five months, and separate from their mother at about one to two years. Snow leopards are sexually mature at two to three years old (Nowell & Jackson, 1996).

Morphology

Snow leopards have thick, cream or pale yellow fur with dark rosettes. Their head is shorter, broader, and smaller relative to body size than other big cats (Fox, 1989). Nasal bones are broad and the nasal cavity is relatively enlarged, which is hypothesised to be an adaptation to cold climates (Hemmer, 1972). Other adaptations to the mountainous climate the snow leopard inhabits are its long tail—used for thermoregulation, balance, and communication—and long hind legs that facilitate movement on steep mountainsides.

Natural history

There is some debate over snow leopards' line of descent, but the most recent genetic study shows them diverging from other species of the Panthera genus, along with lions, about 4.63 million years ago. Although their historic range was about

15% larger than it is now ("Panthera Snow Leopard Program", n.d.-c), it was still characterized by mountainous regions in which the snow leopard specializes.

Ecology

Snow leopards can be found in 12 countries in central Asia, including Afghanistan, Bhutan, China, India, Kazakhstan, Kyrgyz Republic, Mongolia, Nepal, Pakistan, Russia, Tajikistan, and Uzbekistan (Fox, 1994). They are adapted to the cold mountainous regions of these countries, which are defined by arid and semi-arid shrub-land, grassland, or barren areas (Jackson, 1996). Snow leopards commonly overlap each other's ranges, but avoid one another through signs such as marking (Ahlborn & Jackson, 1986; Jackson, 1996).

Threats

The main threats to the snow leopard population are persecution and poaching, decrease in prey abundance, and habitat loss ("Panthera Snow Leopard Program," n.d.-c), in that order of impact. Specific to region, human conflict is the main source of threat in the Himalayas, the Karakorum, and the Hindu Kush mountains, while poaching affects the central Asian and northern regions more (Theile, 2003).

Persecution and poaching

As habitats decrease, animals often venture into human habitation to find prey. Snow leopards, facing a decrease in prey, sometimes target livestock, often killing many animals at a time (5 to 100 in one night; Jackson & Wangchuk, 2001). Livestock owners are often economically devastated by the loss of animals, and uneducated about how to block attempts at predation, as well as the conservation status of the snow leopard; in addition they are often compensated poorly by the

government for their loss (Jackson & Wangchuk, 2001). As a result they often retaliate, killing the snow leopards that they think are responsible.

Snow leopards also suffer from what seems to be an increasing illegal trade in pelts and bones. For example, in the Xinjiang Autonomous Region in western China alone, it is estimated that 20-30 snow leopards are poached each year (Dai, 2002), while 100 animals are thought to have been poached since 1990 in Qinghai Province (Theile, 2003).

Decrease in prey

Although humans don't tend to live in snow leopard habitat, their livestock graze in it, leaving less food for the snow leopard's natural prey. For example, in the Spiti Valley in the Indian Trans-Himalaya, there is evidence that a number of species, including the wild yak (*Bos grunniens*), kiang (*Equus kiang*), Tibetan argali (*Ovis ammon hodgsoni*), and chiru, or Tibetan antelope (*Pantholops hodgsonii*), may have been driven to extinction due to this phenomenon (Mishra et al., 2002). In addition, humans represent competition for similar prey (Schaller et al., 1988). A decrease in prey populations translates into a decrease in snow leopard populations. Poisoning of prey items such as rodents, which are seen as vermin, affect the snow leopard population as well (Theile, 2003). This decrease in prey acts indirectly on snow leopard populations as well: if the cats are forced to prey upon livestock to increase their food intake, retaliation often occurs.

Habitat loss and fragmentation

Although snow leopards can be found in 12 countries, their distribution is low, occupying 1.6 million km^2 of a 2.3 million km^2 habitat (Jackson & Hunter, 1996). Decreases in habitat can be due to development, resource extraction, or road building. In addition, conflict often affects animals negatively. For instance, during

the recent war in Afghanistan, guerrillas targeted for air raids hid in snow leopard habitat (Zahler & Graham, 2001).

Genetics

There exists some debate as to the exact relationships within the Panthera genus. However, recent research has found that the snow leopard is the sister species of the lion—that is, they diverged from a common ancestor at the same time, about 4.63 million years ago, representing the latest divergence within Panthera (Wei et al., 2011). Because of morphological similarities, the snow leopard was often thought to be more closely related to the cheetah. However, DNA analysis suggests that convergent evolution may be a better explanation for their similar vocal cords, which are different from all other species of cat (Wei et al., 2011).

The African lion (*Panthera leo*)

Genetically the sister species to the snow leopard, African lions, which speciated last in the subfamily Pantherinae, are labelled Vulnerable by the IUCN Red List, with a decreasing population trend. Recent estimates of African lions remaining in the wild range from 16,500-30,000 (Bauer & Van Der Merwe, 2004), a number that is 55-70% lower than an estimate in 1996 (Nowell & Jackson, 1996). New research estimates that nearly half of the lion populations in Africa will decline to near extinction within the next 40 years, unless steps are taken to avert this decimation (Packer et al., 2013).

Biology

The tallest, and the second largest cat after the tiger, lions weigh from 126-181kg (Nowell & Jackson, 1996). Body length ranges from 140-250cm and height from 107-123cm (Haas et al., 2005). They are tawny in colour and the males have a mane the

growth of which is influenced by testosterone (Haas et al., 2005). In the wild, lions live up to 12-18 years, and in captivity up to 30, although the average age of death is 13 (Nowell & Jackson, 1996). The most distinct characteristic of the lion is that it is an overtly social species, unlike any other living cat species. While there is no clear reason for this strategy to exist in only one species, recent research suggests that territorial competition, which affects reproductive success and mortality, may play an important role in the evolution of sociality in lions (Mosser & Packer, 2009), who live in higher densities than other felid species and therefore experience more competition for space.

Diet

Lions generally prey upon large ungulates, including buffalo (*Syncerus caffer*), zebra (*Equus quagga*), wildebeest (*Connochaetes*), and more, but like all cat species, they are opportunistic hunters and will also eat rodents and even elephants (*Loxodonta*; Nowell & Jackson, 1996).

Reproduction

While there is no set seasonality in lions, they tend to have birthing peaks from March to July, and produce one to four cubs after an average of 110 days gestation (Nowell & Jackson, 1996). Males leave the pride when they reach 2-4 years old. Some females disperse as well (for example, 33% in the Serengeti; Pusey & Packer, 1987) at around age 2.5, but most are incorporated into the pride. Lions are sexually mature at 24-30 months, but typically start reproducing at 4-5 years old.

Morphology

Generally uniformly tan in colour, individual lions may have some variety of shade of coat. There is some evidence of white lions (a genetic mutation) existing in South

Africa. Lions are the only cats with tufted tails, and with manes (in males). Lions are one of four species—including jaguars, leopards, and tigers—that have the ability to roar.

Natural history

Lions ranged from northern to southwest Africa historically, as well as Europe and India, where a small population (around 400) of Asiatic lions (*Panthera leo persica*) still exists in the Gir Forest sanctuary in Gujarat. Other than that population, they are now mostly restricted to eastern and southern Africa.

Ecology

African lions are now concentrated in a territory reduced by 83% (Ray, Hunter, & Zigouris, 2005), in Botswana, Central African Republic, Ethiopia, Kenya, Tanzania, Zaire, and Zambia (Nowell & Jackson, 1996), with small numbers remaining in the west. Lions are typically found in open woodlands, thick brush, scrub, or grasslands, but are also found in mountainous regions and very arid environments (Nowell & Jackson, 1996). Lions live in prides made up of five to nine females and their cubs, and two to six males. A pride's territory can range from 20-500 km^2, and can overlap with other prides (Haas et al., 2005).

Threats

Persecution

One of the biggest problems for African lions is the human-lion conflict. Because humans often inhabit lion territory, attacks on livestock, and sometimes humans, remain a problem. Both of these can cause retaliatory or pre-emptive killing of lions, the biggest threat to the species (Frank et al., 2006). For example, in Kenya, 76 lion killings have been documented since 2001, and in Tanzania, more than 125 from

2000-2005. These are only the documented amounts—many areas are completely undocumented.

In addition, although trophy hunting is often used as an incentive tool of conservationists, there is evidence that it causes population decline in African lions (among other species) and should be more heavily regulated (Packer et al., 2009).

Habitat loss and prey depletion

Both habitat loss and the subsequent prey depletion are major threats to African lion survival. Severe population decline has been attributed to human settlement and agriculture (Bauer & Van der Merwe, 2004), as well as fragmentation and extirpation (Nowell & Jackson, 1996).

Habitat fragmentation causes lower levels of heterozygosity (Maddock et al., 1996, in Ray et al., 2005), higher levels of abnormal sperm (Packer et al., 1991), and increased chances of vulnerability to disease (Kissui & Packer, 2004), as has been seen in isolated populations of lions in South Africa and in the Ngorongoro Crater region.

Disease and inbreeding

Lions are vulnerable to epidemic disease, due to their social structure (Ray et al., 2005). For instance, 35% of the population (more than 1,000) of Serengeti-Mara lions were killed within six months by canine distemper virus in the early 1990s (Packer et al., 1999). About four years later, they had recovered their original population size. Outbreaks of infection due to fly bites caused a reduction in the Ngorongoro Crater population from 75-100 animals to 12 (Packer et al., 1991). The population then recovered within 13 years, only to start declining again due to other factors. While lions seem to be able to recover from disease outbreak, they are often subject to other threats that, in combination with disease, may cause serious population

decline or hinder recovery. Recently, lions have begun to be infected by bovine tuberculosis—the long-term effects of which are unknown in lions (Ray et al., 2005).

Genetics

As mentioned above (see snow leopard genetics section), research has linked the lion with the snow leopard genetically—the sister species diverged from a common ancestor about 4.63 million years ago, the latest divergence within Panthera (Wei et al., 2011).

2.3 Conclusion

Overall, species biology, natural history, and genetics can inform how personality and well-being data is interpreted and understood. For instance, because personality and well-being are partly genetic, there are selective pressures on them. Therefore, a species' personality structure should, to a certain extent, be based on the specific selective pressures that that species faces within its ecological niche.

Chapter 3

Personality in felids (meta-analysis)

Before carrying out my own analyses on the cat species included in this work, I assessed the state of cat personality research by conducting a meta-analysis on the subject. To begin, I conducted a literature search. Using keywords for cat species including both common and scientific names, and the terms personality and temperament, a literature search was carried out in PsychInfo, CAB Abstracts, and ISI Web of Knowledge (which includes Web of Science, BIOSIS, and Medline). All articles included were from peer-reviewed journals and had to focus on personality directly. In other words, articles that mentioned some sort of personality construct, but did not actually assess personality in cats were not included. For example, Podberscek et al. (1991) conducted a behavioural assessment of laboratory cats in a familiar/unfamiliar person test. However, they were interested in the frequency of behaviours and therefore did not directly address personality constructs, although they included individual variation and dominant behaviour. Similarly, Mertens and Turner (1988) discuss domestic cat individuality in terms of interactions with humans; in fact individuality was the most important factor of those measured influencing their behaviour. However, the terms "shy" and "trusting" are not introduced until Section 5, and there is no explicit definition of those terms—the authors state that it was not their goal to define behavioural profiles.

3.1 Statistical analyses

Following Jones and Gosling's (2005) review of dog research, both reliability and validity of the current research in cat personality was assessed. Reliability, when results occur dependably, is a fundamental measure of consistency (Gosling, 2001). Along with validity, which measures how well an assessment tool is evaluating

what it is meant to determine, reliability reflects the value of the assessment tool being used.

There are different types of reliability, including inter-rater reliability, internal consistency, or test-retest reliability (Jones and Gosling, 2005). Most of the studies in this review measured inter-rater reliability, except where noted. Therefore, minimum and maximum correlations for inter-observer agreement were reported for each study where possible (and percentages for three of the studies). Mean correlations were calculated for each measure used in a study, and the unweighted and sample-weighted means were calculated across studies. While unweighted measures have been said to lead to a better estimate of the variance of the population, and to be a more conservative measure, others have found this is not necessarily the case, and advocate using both measures (Fuller & Hester, 1999). Spearman correlations between measures (for example survey and behavioural observations) were reported for each study that assessed convergent validity, which demonstrates strong correlations among measures assessing one construct. Unweighted and sample-weighted means, and confidence intervals (based on unweighted means; Jones and Gosling, 2005) were calculated for each personality dimension for all species, for domestic cats, and for wild species.

3.2 Results

There are many different personality traits measured in cats, with a few similarities across all species, including those related to activity or extraversion (active, curious, bold, excitable, extraversion, dominance); sociability (friendly, agreeable, social, extraversion); neuroticism (tense, hide, anxious, timid, fearful, staying indoors), and aggression (rough, aggressive). However, there is enough variability in terms, and some terms that were only found once (arrogant/calculating, conscientiousness, intellect/openness, trusting, and calm/self assured), that there is a need to

standardise and validate the terms found, so that a meaningful discussion can be had.

3.3 Types of research

Personality assessment

While assessment methods were varied, there were some consistencies in personality and behavioural methods (Table 2). Among animals in zoo environments, surveys were always used. Half of those studies also used behavioural tests: a novel object (Gartner & Powell, 2012) and a mirror stimulation (Wielebnowski, 1999) test. Research facilities generally carried out some sort of behavioural assessment (observations, novel object tests, and unfamiliar person tests), with only two using a survey (Feaver et al., 1986; Turner et al., 1986). Finally, research conducted in private homes generally used behavioural observations or surveys, with two carrying out novel object tests (Durr and Smith, 1997; Meier and Turner, 1985).

Research goals

The studies varied in their goals as well (Fig. 4). Most of the zoo studies had a similar goal—to increase the welfare of the animal. On the other hand, research facilities mainly addressed how to reduce stress that leads to aggression toward handlers, although one (Siegford et al., 2003) addressed understanding personality as a goal to increasing adoption rates, and two looked at paternity and development (McCune, 1995 [and socialisation]; Turner et al., 1986). The largest group, studies based on free-ranging cats or those already placed in homes, had varying goals including understanding individual differences and their implications (Bradshaw and Cook, 1996; Feaver et al., 1986; Lee et al., 2007; Lowe and Bradshaw, 2001; Meier and Turner, 1985; Natoli et al., 2005; van den Bos and de Vries, 1996), social

dominance (Durr and Smith, 1997; van den Bos and de Cock Buning, 1994), assessing and solving problems of methodology (Gosling and Bonnenburg, 1998), and understanding human-cat interactions (Wedl et al., 2011; Zeigler-Hill and Highfill, 2010).

Age

Zoo studies had a large range of ages as zoos keep animals until they die (n=131, M=7.95 years, SD=2.25). Domestic cat studies either did not report age (n=5), or, excepting one, looked at young animals, up to 4 years (n=62, M=4.83 years, SD=2.09). Bradshaw and Cook (1996) recorded age ranges (6 months to over 8 years) as owners were not always sure about exact ages. Lowe and Bradshaw (2001) tested animals at age 4, 12, and 24 months (n=29). Feaver et al. (1986) tested two groups of seven cats (Group 1: M=5.1, range=2.5–6; Group 2: M=4.7, range=3–6.5). Van den

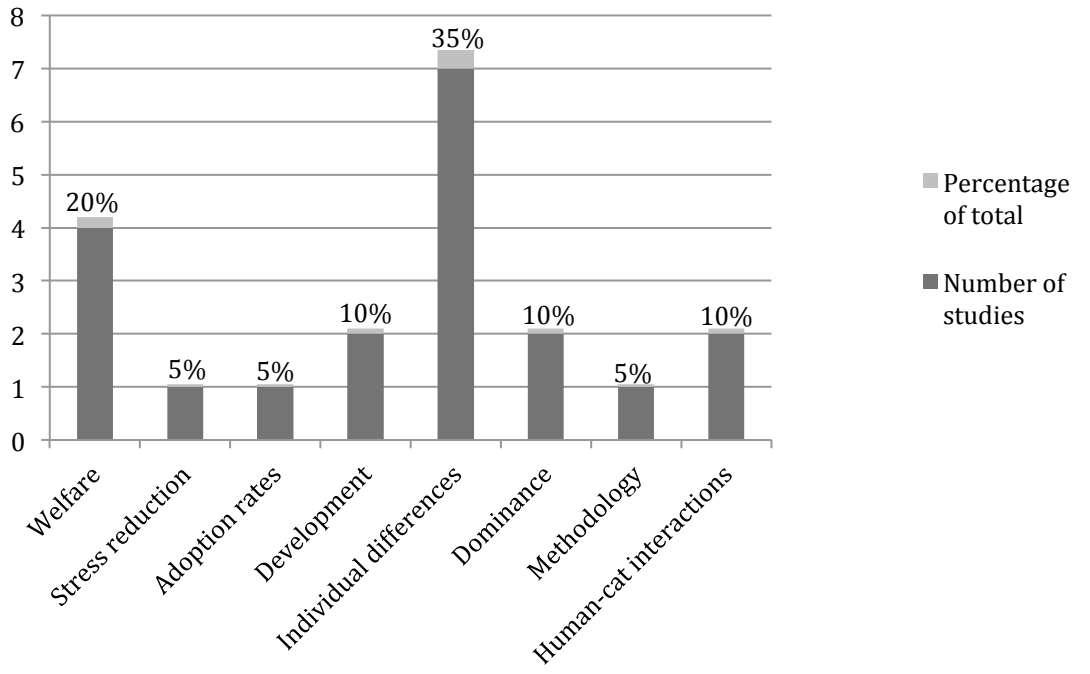

Figure 4 Research goals of the cat personality studies reviewed, in percentage of the total and total number out of 20.

Table 2 Summary of published felid personality research

Author	Species	Sample Size	Sex	Age	Environment	Methodology
Bradshaw & Cook, 1996	Domestic cat	36	17M/19F	6 mo.-over 8	Privately owned	Behavioural observations/survey
Durr & Smith, 1997	Domestic cat	22	9M/13F	5-11yrs	Privately owned	Novel object/unfamiliar animal/ object dominance
Feaver et al., 1986	Domestic cat	14	Female	2.5-6.5	Research facility	Survey/Behavioural observations
Gartner & Powell, 2012	Snow leopard	11	4M/7F	2-19yrs	Zoo	Survey/novel object
Gosling & Bonnenburg, 1998	Domestic cat	440	NR	NR	Privately owned	Survey
Iki et al., 2011	Domestic cat	8	Male	2.75yrs (onset)	Research facility	Tester interaction, ACTH test, behavioural, surgery
Lee, Ryan, & Kreiner, 2007	Domestic cat	196	NR	NR	Privately owned	Survey
Lowe & Bradshaw, 2001	Domestic cat	29	16M/13F	Birth-2yrs	Privately owned	Behavioural observations
McCune, 1995	Domestic cat	37	19M/18F	Birth-1yr	Research facility	Novel object/unfamiliar person
Meier & Turner, 1985	Domestic cat	62	NR	NR	Privately owned	Novel object/unfamiliar person
Natoli et al., 2005	Domestic cat	45	Male	NR	Free- ranging	Behavioural observations
Phillips & Peck, 2007	Bengal tiger	7	6M/1F	2-9yrs	Zoo	Survey
Reisner et al., 1994	Domestic cat	32	NR	5-20wks	Research facility	Handling during socialisation/ACTH test
Siegford et al., 2003	Domestic cat	20	Female	10-18mo	Research facility	Novel object/unfamiliar person
Turner et al., 1986	Domestic cat	40	NR	NR	Research facility	Survey
van den Bos & de Cock Buning, 1994	Domestic cat	10	Female	2-4yrs	Research facility	Behavioural observations
van den Bos & de Vries, 1996	Domestic cat	25	Female	1-5yrs	Research facility	Behavioural observations
Wedl et al., 2001	Domestic cat	40	25M/15F	9mo-13yrs	Privately owned	Survey/behavioural observations
Wielebnowski, 1999	Cheetah	44	19M/25F	3-13yrs	Zoo	Survey/mirror test
Wielebnowski et al., 2002	Clouded leopard	72	36M/36F	3-18yrs	Zoo	Survey
Zeigler-Hill & Highfill, 2010	Domestic cat	106	NR	NR	Privately owned	Survey

NR: Not reported

M: Male; F: Female

ACTH: Adrenocorticotropic hormone

Bos and de Vries (1996) tested 29 cats, with ages ranging from 0.3 to 5 years. Research facilities all used young animals, under 3 years old (n=121, M=1.55 years, SD=1.60).

Environment

There were four types of environment in the studies—research facilities (38% of studies), home environments (38% of studies), free ranging (~5% of studies), and zoos (19% of studies). It is unknown whether environment plays a role in the behaviour or personality of cats, but it is one possible explanation for the variance in results in the domestic cat, as personality is not completely comprised of genetic makeup (Bell and Sih, 2007; Sih et al., 2004).

Breed and subspecies

Domestic cat breed was either not identified (n=11) or domestic short-haired cats were studied (Iki et al., 2011; McCune, 1995; Siegford et al., 2003; van den Bos and de Cock Buning, 1994; van den Bos and de Vries, 1996; Wedl et al., 2011 [plus two domestic long hairs]). The subspecies of tiger studied was the Bengal tiger (Phillips and Peck, 2007); the other zoo animals do not have subspecies.

Sexual status of subjects

Zoo animals were all intact, since breeding is a primary reason to keep endangered animals. Some of the domestic cats were intact, while some were neutered/spayed. Some studies specified how many of each; some did not. Personality assessment after such operations may be an important construct, especially in shelter situations, where animals are almost always neutered/spayed, and where personality may play a role in adoption rates (Siegford et al., 2003); however, there is no evidence that this plays a role in personality.

3.4 Are the measures reliable?

Only 60% of the studies reported reliability of any kind. Six of these reported inter-observer agreement (Table 3). Six studies were not included in Table 3 because of the different methods they used to assess reliability. Two studies used Cronbach's alpha as a measure of internal consistency of each dimension measured across subjects (Gartner & Powell, 2012: M=0.85 [but also reported correlations and was therefore included in Table 3]; Zeigler-Hill and Highfill, 2010, M=0.85[3]). One used percentages of positive and negative results for the Feline Temperament Protocol (FTP; 88% and 92%, respectively) and percentages of intra- and inter-rater agreement for behavioural observations of two cats during a stress test (91% and 89%, respectively; Iki et al., 2011).

Meier and Turner (1985) showed test-retest reliability using frequencies, but did not report numerical values. Thirty-three of the cats in the study were encountered at least three times each in the behavioural analysis. Of these, 25 always had the same reaction: nine could always be stroked, 16 always ran away. Based on these behaviours, the authors assessed two types of personality: shy and trusting.

Siegford et al. (2003) reported test-retest reliability for the FTP. The FTP measures general levels of sociability ("acceptable scores") and aggressiveness and adaptability to new situations ("questionable scores"; Lee et al., 1983). There was no statistically significant change over time for acceptable scores ($F[3,76]=1.29$, $p=.28$), while questionable scores changed significantly over time ($F[3,76]=6.01$, $p=.001$): six months after adoption, cats had lower questionable scores than second pre-adoption and 3 months post-adoption tests. However, while the authors reported high inter-observer reliability, they gave no numerical value. They did, however, report that

[3] This study reported an internal consistency coefficient, without specifying what type.

Table 3 Inter-observer agreement (reliability) measures in felid personality assessment (Spearman's rho, except where noted)

Study	Inter-observer agreement					Number of items/*n*
	Mean/SE	Maximum		Minimum		
		Correlation	Item label	Correlation	Item label	
Durr & Smith, 1997	.56/.23	.84[a]	Novel stimulus (group)	.28[a]	Novel stimulus (individual)	7/22
Feaver et al., 1986	.63/.30	.91	Sociable with people	.31	Solitary	18/14
Gartner & Powell, 2012	n/a	.96[a]	Not specified	.60[a]	Not specified	21/11
Turner et al., 1986	n/a	.96/.90	Friendliness to humans (mothers/juveniles)			1/16
Turner et al., 1986	n/a	.74/.43/.48/.47	Friendliness to humans (juveniles)			1/25
Turner et al., 1986	n/a	.72	Friendliness to humans (mothers)			1/22
Wielebnowski, 1999	.75/.16	.98[a]	Eccentric	.57[a]	Eccentric	18/44
Wielebnowski et al., 2002	n/a/.12	.92[a]	Not specified	.37[a]	Not specified	13/72
Unweighted mean	.65					
Sample-weighted mean	.68					

Note: Only studies that specified all item correlations were included in the mean correlation (including unweighted and sample-weighted means)

n=sample size, a=Kendall correlation coefficients

mean acceptable scores on all FTPs were negatively correlated with mean questionable scores (r=-0.85, p<.001).

Wedl et al. (2011) reported the inter-observer agreement as .80, but gave no further details. Another study (Phillips and Peck, 2007) reported using Friedman's test (Friedman, 1937)—a non-parametric measure similar to repeated measures ANOVA, but only reported the p value.

Minimum correlations across the remaining studies ranged from .28 to .60 and maximum correlations ranged from .84 to .98. The sample weighted mean was 0.68, but this could only be calculated on three studies, due to the lack of available data. Mean inter-rater reliabilities varied from .56 to .75 for these three studies. It is clear that there is reliable inter-rater agreement on many of the items researched; however, enough studies did not include the statistics, and enough had low correlations so that overall reliability cannot be verified across these cat personality studies.

3.5 Are the findings valid?

Fifty-five percent of the studies measured validity. The convergent validities for Sociable, Dominant, Curious, and Active were strong. The convergent validities for Aggressive, Calm, Timid/Fearful, and Excitable were less so (Tables 4 and 5).

Table 4 Convergent validities for the felid personality dimensions

Dimension	UM	95% CI	SWM
Sociable	.94	.88, .94	.93
Dominant	.76	.68, .81	.74
Curious	.75	.65, .83	.70
Active	.72	.49, .79	.49
Aggressive	.57	.28, .78	.48
Calm	.40	.16, .64	.40
Timid	.36	.22, .49	.34
Excitable	.34	.21, .47	.34

UM=unweighted mean; SWM=sample-weighted mean; CI=confidence interval

Table 5 Convergent validity in felid personality assessment

Dimension study	Trait	Criterion measure		Validity coeff.	95% CI	Sample size
		Type of test	Basis for scoring			
Active						
Gartner & Powell, 2012	Active/Vigilant	Novel object test	Number of visits to object	.74		11
			Time spent locomoting	.75		
			Time spent exploring	.75		
Phillips & Peck, 2007	External awareness		Number of approaches by keepers	.86		7
Wedl et al., 2011	Active	Behavioural observations	Non-overlapping patterns	.91		40
			Non-overlapping patterns per minute	.93		40
			Event type complexity	.93		40
Wielebnowski, 1999	Active	Novel object test (mirrors)	Number of approaches	.55		44
			Sniff	.35		
			Stare	.35		
			Growl/Hiss	.61		
			Approach time	-.25		
Wielebnowski et al, 2002	Pace	Fecal corticoid concentrations		.35		72
Unweighted mean				.72	.49, .79	
Sample-weighted mean				.57		
Aggressive						
Feaver et al., 1986	Aggressive	Behavioural observations	Stare+Hit+Chase	.85		14

Dimension study	Trait	Criterion measure		Validity coeff.	95% CI	Sample size
		Type of test	Basis for scoring			
Wielebnowski, 1999	Aggressive to conspecifics	Novel object test	Growl/Hiss	.59		44
	Aggressive to people		Number of approaches	.45		
			Stare	.32		
			Growl/Hiss	.44		
Unweighted mean				.57	.28, .78	
Sample-weighted mean				.48		
Calm						
Wielebnowski, 1999	Calm	Novel object test	Stare	-.38		44
			Growl/Hiss	-.31		
			Approach time	-.50		
Unweighted mean				.40	.16, .64	
Sample-weighted mean				.40		
Curious						
Durr & Smith, 1997	Attention span	Behavioural observations	Latency of approach	.76 (Group 1)		11
				.88 (Group 2)		11
Feaver et al., 1986	Playful	Behavioural observations	Play	.60		14
Gartner & Powell, 2012	Curious/Playful	Novel object test	Number of visits to object	.79		11
		Novel object test	Time spent locomoting	.77		
		Novel object test	Time spent exploring	.73		
Wielebnowski, 1999	Curious	Novel object test	Approach time	-.62		44
Unweighted mean				.75	.65, .83	
Sample-weighted mean				.70		

Table 5 *continued*

Dimension study	Trait	Criterion measure		Validity coeff.	95% CI	Sample size
		Type of test	Basis for scoring			
Dominant						
Durr & Smith, 1997	Dominant	Novel object test	Latency to approach	.72 (group 1)		11
				.90 (group 2)		11
Natoli et al., 2005	Proactive	Social rank		.71		14
		Social rank		.67		10
		Social rank		.77		21
		Reproductive success		-.73		14
		Reproductive success		-.68		21
van den Bos & de Cock Buning, 1994	Agonistic (offensive threats)	Behavioural observations	Rank	.80		10
Unweighted mean				.76	.68, .81	
Sample-weighted mean				.74		
Excitable						
Wielebnowski, 1999	Excitable	Novel object test	Number of approaches	.35		44
			Approach time	.33		
Unweighted mean				.34	.21, .47	
Sample-weighted mean				.34		
Self Assured						
Wielebsnowki, 1999	Self-assured	Novel object test	Approach time	-.50		44
Shy						
Meier & Turner, 1985	Shy		Fleeing	.38		26

Dimension study	Trait	Criterion measure		Validity coeff.	95% CI	Sample size
		Type of test	Basis for scoring			
Sociable						
Feaver et al., 1986	Sociable with people	Behavioural observations	Approach+Sniff+Head and Body rub observer	.69		14
McCune, 1995	Friendly-fathered (bold)	Familiar person test	Latency to 1m	.97		37
			Latency to 50cm	.97		37
			Latency to touch	.95		37
			Latency to rub	.95		37
			Number of rubs	.86		37
			Total time<1m	.97		37
			Number of vocals	.93		12
	Socialised		Latency to 1m	.95		37
			Latency to 50cm	.95		37
			Latency to touch	.97		37
			Latency to rub	.96		37
			Total time<1m	.95		37
			Number of vocals	.95		12
	Friendly-fathered (bold)	Stranger approach test	Latency to 1m	.97		37
			Latency to 50cm	.96		37
			Latency to touch	.90		12
			Number of rubs	.89		12
			Total time<1m	.96		37
	Socialised		Latency to 1m	.97		37
			Latency to 50cm	.94		37

Table 5 *continued*

Dimension study	Trait	Criterion measure		Validity coeff.	95% CI	Sample size
		Type of test	Basis for scoring			
			Latency to touch	.96		12
			Latency to rub	.94		12
			Number of rubs	.90		12
			Total time<1m	.94		37
			Number of vocals	.95		12
	Friendly-fathered (bold)	Novel box test	Latency to emergence	.94		12
			Latency to 1m	.97		37
			Latency to 50cm	.95		12
			Latency to touch	.98		12
			Number of times in box	.97		12
			Part body in box	.97		12
			Whole body in box	.97		12
			Total time in box	.90		12
			Total time<1m	.97		12
	Socialised	Novel box test	Latency to emergence	.94		12
			Number of vocals	.91		12
van den Bos & de Cock Buning, 1994	Affiliative	Behavioural observations	Rank	.66		10
	Social licking	Behavioural observations	Rank	.71		10
	Social rubbing	Behavioural observations	Rank	.66		10
Wedl et al., 2011	Sociable	Behavioural observations	Number of patterns	.90		40
			Number of patterns/minute	.90		40
			Non-overlapping patterns	.96		40

Dimension study	Trait	Criterion measure		Validity coeff.	95% CI	Sample size
		Type of test	Basis for scoring			
	Social sniffing	Behavioural observations	Rank	.56		10
			Non-overlapping patterns/ minute	.96		40
Unweighted mean				.94	.88, .94	
Sample-weighted mean				.93		
Subordinate						
van den Bos & de Cock Buning, 1994	Agonistic (defensive threats)	Behavioural observations	Rank	-.79		10
Timid/Fearful						
Wielebnowski, 1999	Fearful of conspecifics	Novel object test	Approach time	.52		44
	Fearful of people	Novel object test	Stare	.27		
	Fearful of people	Novel object test	Approach time	.40		
Wielebnowski et al, 2002	Tense	Fecal corticoid concentrations		.33		72
	Hide	Fecal corticoid concentrations		.25		
Unweighted mean				.36	.22, .49	
Sample-weighted mean				.34		
Vocal						
Feaver et al., 1986	Vocal	Behavioural observations	Chirp+Cry+Mew+Hiss+Growl	.67		14
Voracious						
Feaver et al., 1986	Voracious	Behavioural observations	Eat/Drink	.75		14

CI=confidence interval
Coeff.=coefficient

Six personality dimensions were measured by more than one study: Active, Aggressive, Curious, Dominant, Sociable, and Timid/Fearful. The mean validity coefficient for these dimensions was .68. Dimensions found in single studies included Calm, Excitable, and Self Assured (Wielebnowski, 1999), Shy (Meier and Turner, 1985), Subordinate (van den Bos and de Cock Buning, 1994), and Vocal and Voracious (Feaver et al., 1986). The validity measures are included in Table 4 for these studies, but means and confidence intervals were only calculated for Calm and Excitable, because multiple measures were used.

Siegford et al. (2003) reported validity data, but because they were using the FTP as a measure, the results were not included in this analysis. This is because the FTP only measures general levels of sociability and aggressiveness and adaptability to new situations. However, the results are still pertinent. They found that acceptable (sociability) scores on pre-adoption FTPs positively correlated with positive responses to familiar caretakers in rooms in which the cats were usually housed ($r=.51$, $p=.02$) and average percent of time spent near unfamiliar people in open field tests in novel rooms (men: $r=.60$, $p=.01$; women: $r=.57$, $p=.01$). They also found a positive correlation between questionable (aggressiveness/ adaptability) scores on pre-adoption FTPs and percent of time cats spent in corners of the novel room during open field tests ($r=.51$, $p=.03$). Finally, the number of cell crossings in open field tests positively correlated with acceptable scores on pre-adoption FTPs ($r=.54$, $p=.02$).

Iki et al. (2011) also used the FTP as a measure of personality, but found no behavioural correlates with it. However, acceptable scores correlated significantly with cortisol concentration during a spray bath stress test ($r_s=.70$, $p=.047$); that is, more social cats had higher levels of cortisol during the stress test.

To assess whether the four studies on wild cats affected the results, validity was calculated for domestic cats and wild cats separately. For the wild cats, Active/Vigilant, Curious, and Timid/Fearful were assessed by more than one

study. The convergent validities of these three personality dimensions were similar to the overall numbers reported above: Active/Vigilant (unweighted mean (UM)=.60, sample weighted mean (SWM)=.45, CI at 95%=.40–.71) and Curious (UM=.73, SWM=.68, CI at 95%=.61–.85). Timid/Fearful was not measured in domestic cats so the numbers did not change.

For the domestic cats, Curious/Playful, Dominant, and Sociable were measured by more than one study. Only Curious/Playful was measured in all species; for domestic cats alone, the means were similar to the overall and the wild cat results (UM=.77, SWM=.73), but the confidence interval was quite large (at 95%=.40–1.10) and the upper bound exceeded 1, indicating non-significance. This is probably due to the fact that this measure was only included in two studies. The environments were different, with one taking place in a research facility (Feaver et al., 1986) and one in the home (Durr and Smith, 1997). This may have influenced the results. In addition, Feaver et al. (1986) were measuring "Playful" while Durr and Smith (1997) were measuring "Attention Span"—it is possible that these two things were not similar enough to include in the same category.

3.6. Discussion

Of the studies reported here, 60% included information on reliability. Reliability varied greatly across personality dimensions and both within and across studies, although mean correlations were over .60. Some studies did not include numerical information, and some did not include enough descriptive information. However, compared with similar reviews on dogs (~19%) (Jones and Gosling, 2005) and primates (~10%) (Freeman and Gosling, 2010), there is a reasonable amount of reliability statistics being reported in felid personality research. However, reliability should be a requisite for personality research, so the aim is to have all of the studies including this information. Most of the studies in this review measured inter-rater

reliability. It would be useful for future studies to include this information, but also internal consistency (only two studies in this review did so), as well as test-retest reliability, to provide a better picture of how reliable each measure is within and across studies. Measures that were not used at all in these studies, but have been shown to be effective in primate studies (e.g., Weiss et al., 2006) include intraclass correlations (Shrout and Fleiss, 1979) for continuous measures and Cohen's kappa (Cohen, 1960) for categorical measures. It is clear from the results that personality studies in domestic cats need to report reliability and validity coefficients more consistently.

Convergent validity on some personality dimensions was strong. The dimensions with the highest validity for all species were Sociable, Dominant, and Curious. These were followed by Aggressive, Calm, Timid/Fearful, and Excitable. For wild cats alone, Curious had the highest validity, followed by Active/Vigilant, and Timid/Fearful, and for domestic cats Sociable did, followed by Curious and Dominant. There were seven dimensions only found in one study each. One each of these was found in two wild species—this may explain why they were not present in domestic cats or the other wild species. Two of the remaining five, "Rubbing" and "Feeding" were based more on single behaviours, and therefore cats in other studies may not have had the opportunity to present this type of behaviour, or alternatively, the authors of other papers may not have measured this type of behaviour. Similarly, "Arrogant/Calculating," was only measured in one study—this study was the only one to utilise the Interpersonal Adjective Scales-Revised survey (Wiggins, 1995). The remaining two studies utilised a survey based on the Five-Factor Model (Digman, 1990) and therefore found "Conscientiousness," and "Intellect/Openness," which would not have been measured in other studies. These examples show the importance of measuring personality in a consistent way in order to compare results among studies. This is not to say, however, that one test should be favoured over another, or just one type of test used. Instead, when

conducting such research, an examination of work that has come before may help to minimise the amount of overlap in terminology meaning similar things, and to include as much descriptive information as possible.

Across some behavioural observations, novel object tests, and surveys, reasonable consistency has emerged for certain traits (although not all), and some personality dimensions seem to be consistent. However, because there are differences throughout the research in types of measurement and dimension names, there is no conclusive definition of cat personality established by these studies, nor is there one single method for assessing it that has proved to be reliably consistent.

In addition to the variety of methods used, there are also some limitations to the measures. Surveys are generally well-accepted and validated ways of assessing animal personality—indeed, more reliable than behavioural observations and less subjective than often assumed (Vazire et al., 2007)—as long as the people evaluating the animals have worked with the animals for a long enough period of time (Gosling, 2001). This does not represent a problem in studies of privately owned animals, then, but for those carried out in zoos, and especially free-ranging colonies and research facilities, how long a caretaker has spent with an animal should be noted. All the studies assessed here addressed this issue, although sometimes without stating the actual amount of time spent with the animals.

Only four of the studies used behavioural observations as the only form of assessment. This type of method has the potential problem of assessing behaviours taken out of context (Vazire et al., 2007), so amount of time spent carrying out the observations—and consistency of when and where the observations are carried out—is important. This was addressed in the studies assessed in this review by retesting over years, or long hours of observations—none less than three months. Another potential problem with behavioural observations is the effect the researcher may have on the animal. This is rarely addressed in personality studies, and should be assessed for its possible impact on results.

The convergent validity of personality may be an artefact arising from the fact that, in many studies, the person rating the animal is the same one conducting behavioural observations. However, findings that validation across methods works well regardless of whether the person doing the rating is the same person doing the observing (e.g., in deer, Bergvall et al., 2011), indicate that this is unlikely. Still, it is important that studies show inter-observer agreement, and, where possible, use independent observers and raters.

One problem that often occurs in non-human animal studies for practical reasons is small sample size. The largest sample size among these studies was 440 (an outlier: the next largest was 196, then 106), the smallest 7 (mean n=63.2, SD=98.70). However, if this is taken into account while designing statistical analysis, problems should be minimised. Nevertheless, it may be hard to generalise out to the species level, for example, especially when demographic information (all one gender in a particular study, for example) is inconsistent.

There is evidence of age effects on some animal personality dimensions (e.g., Weiss et al., 2007), and that personality traits may be plastic (e.g., Frost et al., 2007). Most of the domestic cat studies focused on young animals, so future studies should include a wider range of ages or longitudinal designs to see how age may affect personality. These results may influence how we characterise personality in different species—for instance, animals with longer maternal care may show differing effects on personality than those without.

Breed was rarely included or noted in the domestic cat studies. Since there has been some work suggesting behavioural differences between pure-bred and non-pedigree cats (Turner, 2000), and dogs (Duffy et al., 2008; Svartberg and Forkman, 2002) this information should be included in personality studies. Another aspect of domestic cat variability was whether the cat was neutered or spayed. There is no research that looks at the differences in personality in cats that are intact versus those that are neutered or spayed, so this is a possible confound that should

be addressed, as it does seem to play a role in other species, such as dogs (Maejima et al., 2007).

Despite this variability, the studies do seem to be measuring personality, however, or some aspect of it. By using either multiple methods that were correlated, surveys that aggregate knowledge of time and context, or test-retest reliability, the studies avoided measurements at one point in time, or during only one context. Therefore, comparisons among the studies, as shown by the relatively high levels of correlation, can be considered valid, although it would be preferable to have a consistent method of measure across a number of studies with a variety of contexts to more definitively say that these constructs are describing cat personality.

3.7 Conclusions

Felid personality dimensions with high validity for all species are Sociable, Dominant, and Curious. The methods used for studying personality—behavioural observations, novel object tests, surveys—are reasonably reliable, but more work needs to be done due to the variability of methods, small sample sizes, and singular context. Future studies need to include breed information, greater age range, and information on whether individuals were spayed or neutered. While the past three decades have seen an increase in the amount of felid personality research, much more work needs to be done, especially in wild species, where the practical applications of such work could have far-reaching effects for welfare, and ultimately, conservation.

Chapter 4

Methodology

4.1 Methods

All the zoos and shelters involved and the University of Edinburgh gave ethical approval for this research. All caretakers were instructed not to discuss the surveys or their ratings.

4.1.1 Species and rater information

Scottish wildcats and raters

Subjects included 25 Scottish wildcats from three zoos. The age of the subjects ranged from 1 to 15 years (M=3.67 ± 3.14 SD). There were eight wildcats (3 males; 5 females) at Port Lympne Wildlife Centre (PL), in Lympne, Kent, UK; nine wildcats (2 males; 5 females, 2 unknown) at the Highland Wildlife Park (HWP), Kincraig, Kingussie, UK; and eight wildcats (4 males; 4 females) at the British Wildlife Centre (BWC), in Lingfield, Surrey, UK.

Eight caretakers rated the wildcats on two surveys (PL: n=3, HWP: n=3, and BWC: n=2). The caretakers knew the wildcats on average for 2.34 years (PL: M=2.83 ± .56 SD; HWP: M=1.57 ± .60 SD; BWC: M=4.5 ± .3.54 SD).

Domestic cats and raters

Subjects included 100 domestic cats from two shelters. The age of the subjects ranged from 1 month to 19 years (M=4.85 months ± 4.64 SD). There were 85 cats (39 males, 44 females, 2 unknown) at Cats Protection (CP) in Kirkintilloch, Scotland, UK; and 15 cats (6 males; 9 females) at KittyKind (KK) in New York, New York, US.

Twenty-one caretakers rated the domestic cats on two surveys (CP: n=6; KK: n=15).

Clouded leopards and raters

Subjects included 16 clouded leopards from two zoos. The age of the subjects ranged from .49 to 9.58 years (M=4.77 ± 3.39 SD). There were 11 clouded leopards (5 males; 6 females) at Nashville Zoo in Nashville, TN, US (NZ); and 5 clouded leopards (2 males; 3 females) at Port Lympne Wildlife Centre (PL), in Lympne, Kent, UK.

Seven caretakers rated the clouded leopards on two surveys (NZ: n=4, PL: n=3). The caretakers knew the wildcats on average for 6.14 years (NZ: M=2.02 ± 1.04 SD; PL: M=11.67 ± 12.90 SD [individual number of years 1, 8, and 26]).

Snow leopards and raters

Subjects included 17 snow leopards from three zoos. The age of the subjects ranged from 1 to 15 years old (M=6.56 ± 4.68 SD). There were 11 snow leopards (6 males; 5 females) at the Bronx Zoo (BZ), in Bronx, New York, US (four of these animals were included in a previous study: Gartner & Powell, 2012); 4 snow leopards (3 males; 1 female) at ABQ BioPark (ABQ), in Albuquerque, New Mexico, US; and 2 snow leopards (1 male; 1 female) at Norden's Ark (NA), in Bohuslän, Sweden.

Nine caretakers rated the snow leopards on two surveys (BZ: n=6, ABQ: n=2, NA: n=1). The caretakers knew the snow leopards on average for 3.65 years (BZ: M=2.4 ± .85 SD; ABQ: M=4.89 ± 2.65 SD; calculation doesn't include NA, since there was only one caretaker, who knew her charges for 6 years).

African lions and raters

Subjects included 21 African lions from two zoos. The age of the subjects ranged from 3 to 15 years old (M=11.52 ± 3.39 SD). There were 13 lions (3 males; 10 females) at Lion Country Safari (LCS), in Loxahatchee, Palm Beach County, US; and 8 lions (2 males; 6 females) at West Midland Safari Park (WMSP) in Bewdley, Worcestershire, UK.

Seven caretakers rated the African lions on two surveys (LCS: n=3; WMSP: n=4). The caretakers knew the lions on average for 2.17 years (LCS: M=1.5 ± 1.41 SD; WMSP: M=2.5 ± 1.73 SD).

4.1.2 Procedure

The 45- to 52-item (depending on species) personality survey (see Appendix) was based on previous felid personality surveys (Feaver et al., 1986; Gartner & Powell, 2012; Wielebnowski, 1999). Twenty-two traits from the Hominoid Personality Questionnaire (King & Figueredo, 1997) that could be associated with felid behaviour were also included to provide a better overall assessment of personality in conjunction with the other traits. These traits were selected by assessing any overlap with the previous surveys and eliminating duplication. Most of the remaining traits were included, with the exception of certain traits that were deemed unlikely to be assessed well in felids; for example, disorganised, unemotional, or lazy. Any wording specific to primate behaviour was replaced with that describing typical cat behaviour (for example the section of the description of chimpanzee "fearful" that included the words screaming and grimacing was replaced with "retreats readily from conspecifics").

The survey included a specific description to be used for each trait. These traits were rated on a seven-point Likert scale, where one, "not at all," meant the trait did not describe the animal at all, and seven "very much so," meant the trait described the animal to a great degree. In the latter part of the study, seven extra

adjectives were added from the Hominoid Personality Questionnaire for snow leopard personality assessment, to see if they could be validated in cat species (the other felid personality assessments had already been completed).

The four-item subjective well-being survey was developed by King and Landau (2003) for chimpanzees, with an additional keeper social interaction item added to account for animals being housed alone, as described below (see Appendix). The first three items measured overall moods of the wild cats and whether social interactions were enjoyable as opposed to negative, and were meant to assess the balance of positive and negative affect, respectively. Social interactions were divided into two questions, one that addressed social interactions with conspecifics, and one with humans. The fourth item measured personal control, and asked whether the wild cat was effective in achieving its goals. The last item asked how happy the rater would be to be the specific wild cat. These items were rated on a seven-point Likert scale, where one was "least" and seven was "most." (Subjective well-being was not measured in the domestic cats due to timing involved with the shelter environment.) This survey was shown to be reliable in chimpanzees (King & Landau, 2003), orangutans (Weiss et al., 2006), and rhesus macaques (Weiss et al., 2011). In each of these studies, the items were reduced to a single factor, labelled subjective well-being.

4.2 Analyses

All analyses were carried out using IBM SPSS 19 for Macintosh, unless otherwise noted. For both surveys, inter-rater reliabilities were calculated using the intraclass correlation coefficients ICC(3,1) (the reliability of individual ratings) and ICC(3,*k*) (the reliability of the mean ratings of *k* raters) (Shrout & Fleiss, 1979). Items that were not reliable, defined as having an ICC(3,1) and/or an ICC(3,*k*) less than or equal to zero were omitted from further analyses (Weiss et al., 2007; Weiss et al., 2011). ICC(3,1)s were then compared across species.

After identifying the reliable items on both scales, I obtained the means across raters for each item on each animal. I subjected the items to principal components analyses for each scale. The number of components to extract was determined via parallel analysis (Horn, 1965; O'Connor, 2000) and by examining the scree plot. For confirmation, because the sample sizes were small (for all species but the domestic cat), regularised exploratory factor analyses were conducted (Jung & Lee, 2011; Jung & Takane, 2008). This method of factor extraction is designed for small sample sizes. Factor extraction was calculated with MATLAB 7.12.0.635 (R2011a), using a program provided by Sunho Jung. Factor loadings were derived via unweighted least squares and assumed that unique variances did not differ across items. The components were rotated using the varimax procedure in R version 2.15.1 (R Core Team, 2012). ICC(3,1) and ICC(3,*k*) and internal consistency as described by Cronbach's alpha were measured for the personality factors and the subjective well-being measures. ICC (3,1) and ICC(3,*k*) are considered of fair clinical significance if they range from .40-.59; good clinical significance from .60-.74; and excellent clinical significance from .75-1.0 (Cicchetti, 1994, but note that this is offered only as a guideline for judgement).

For the overall taxon personality scale, I standardised the data before running the principal components analysis, in order to avoid confounding the covariation of traits across individuals with covariation across species, following a procedure used in cross-cultural studies of human personality (McCrae, Terracciano, & 78 Members of the Personality Profiles Cultures Project, 2005).

As in previous studies (e.g., Weiss et al., 2006; Konečná et al., 2012), I defined factor loadings $\geq |0.4|$ as salient for the principal components analyses, and $\geq |0.3|$ for the regularised exploratory factor analyses, which yields more conservative loadings. Also as in these prior studies, if an item had multiple salient loadings, I assigned that item to the component that had the highest loading. Based on these

loadings, I created unit-weighted factor scores (Gorsuch, 1983), which I then transformed into *z*-scores.

Finally, factors across species were compared using orthogonal targeted Procrustes rotation (Schönemann, 1966). This method entails rotating one set of factor loadings with another to maximise fit and to minimise the sums of squares of deviations from a target matrix, while maintaining orthogonality (McCrae et al., 1996). Then, factor congruences were calculated to identify matching factors. In this work, Procrustes analyses were carried out using syntax developed by Fischer and Fontaine (2011).

Chapter 5

Results

5.1 Inter-rater reliability

Scottish wildcats

For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from .04 (quitting) to .75 (aggressive to conspecifics), with a mean reliability of .41. The reliabilities of mean ratings, ICC(3,*k*), ranged from .10 (quitting) to .89 (aggressive to conspecifics), with a mean reliability of .59. The ICCs for the items reckless, distractible, and individualistic were all negative, and so these items were excluded from further analysis (see Table 6 for personality ICCs for all species).

For the subjective well-being items, the reliabilities of individual ratings, ICC(3,1), were .24 (be the cat), .26 (pleasure from social interactions), .32 (moods), and .39 (ability to achieve goals). The reliabilities of mean ratings, ICC(3,*k*), were .45 (be the cat), .49 (pleasure from social interactions), .55 (moods), and .63 (ability to achieve goals).

Domestic cats

The reliabilities of the individual ratings, ICC(3,1), ranged from .07 (fearful of conspecifics) to .73 (aggressive to people), with a mean reliability of .35. The reliabilities of the mean ratings, ICC (3,*k*), ranged from .18 (fearful of conspecifics) to .90 (aggressive to people), with a mean reliability of .58. The ICCs for the items quitting, aimless, smart, vigilant and deliberate were all negative, and so were excluded from further analysis.

Table 6 Intraclass correlations for individual (ICC[3,1]) and mean ratings (ICC[3,*k*]) of personality traits for all study species

Trait	Domestic cat		Scottish wildcat		Snow leopard		Clouded leopard		African lion	
	ICC									
	(3,1)	(3,*k*)	(3,1)	(3,*k*)	(3,1)	(3,*k*)	(3,1)	(3,*k*)	(3,1)	(3,*k*)
Active	.55	.79	.34	.58	.53	.82	.36	.67	.27	.56
Affectionate	.38	.65	.12	.26	.20	.50	.36	.66	.10	.28
Aggress.[1] (c)	.45	.72	.75	.89	.22	.54	.15	.38	.39	.69
Aggress. (p)	.73	.90	.59	.79	.54	.82	.80	.93	.33	.63
Aimless	-.08	-.32	.11	.25	-.04	-.19	.31	.61	.31	.61
Anxious	.38	.65	.39	.63	.21	.51	.24	.52	.64	.86
Bold					.00	.01				
Bullying	.58	.81	.63	.82	.03	.11	.21	.49	.53	.80
Calm	.27	.54	.14	.31	.51	.81	.35	.65	.26	.55
Clumsy					.22	.53				
Constrained	.11	.28	.24	.46	.07	.24	.09	.27	.23	.52
Cool	.35	.62	.56	.77	.32	.66	.42	.72	.42	.71
Cooperative	.40	.67	.52	.74	.16	.44	.41	.71	.10	.28
Curious	.54	.78	.55	.76	.43	.75	.38	.68	.17	.42
Decisive	.08	.21	.26	.49	-.01	-.04	-.14	-.76	.16	.39
Defiant					.25	.58				
Deliberate	.01	.02	.34	.58	.04	.13	-.16	-.94	.36	.66
Distractible	.36	.64	-.09	-.27	.21	.51	.48	.76	.04	.11
Dominant	.45	.72	.44	.68	-.08	-.39	.17	.42	.73	.90
Eccentric	.25	.51	.61	.80	.02	.09	.59	.84	.16	.40
Erratic	.23	.48	.36	.60	.24	.55	.54	.80	.32	.62
Excitable	.29	.56	.12	.27	.29	.62	.39	.69	.11	.29
Fearful (c)	.07	.18	.65	.83	.16	.44	.00	-.01	.69	.89
Fearful (p)	.48	.75	.54	.76	.59	.85	.70	.89	.33	.64
Friendly (c)	.29	.56	.32	.56	.37	.70	.19	.45	.08	.24
Friendly (p)	.57	.80	.33	.57	.15	.40	.71	.90	.33	.63
Gentle					.29	.61				
Impulsive	.18	.40	.51	.74	.32	.66	.27	.56	-.04	-.16
Independent	.21	.45	.37	.61	-.07	-.38	.35	.65	.18	.44
Individual	.37	.65	-.07	-.20	.03	.10	.06	.18	.08	.24
Inquisitive					.36	.69				
Insecure	.43	.70	.68	.85	.09	.28	.64	.86	.67	.88
Inventive					.19	.48				
Irritable					.46	.77				
Jealous	.09	.23	.20	.40	.10	.31	.17	.42	.26	.55
Persevering	.09	.23	.35	.59	-.12	-.79	-.04	-.14	.24	.52
Playful	.53	.78	.62	.81	.64	.88	.66	.87	.42	.71
Predictable	.15	.35	.68	.85	.25	.58	.28	.58	-.18	-1.11
Quitting	-.10	-.40	.04	.10	-.05	-.22	-.25	-2.22	.09	.27
Reckless	.11	.29	-.12	-.41	.21	.51	.01	.04	.25	.54
Self-assured	.15	.35	.51	.73	.02	.08	.65	.87	.65	.87
Smart	-.04	-.14	.23	.45	-.09	-.48	.12	.33	.38	.68
Solitary	.66	.86	.28	.51	.24	.55	.44	.73	.40	.70
Stable	.43	.70	.69	.86	.41	.73	.17	.41	.12	.33
Stingy	.28	.55	.29	.52	.20	.50	-.03	-.12	.58	.83
Submissive	.28	.55	.20	.40	.05	.17	.02	.07	.81	.94
Suspicious	.33	.60	.63	.82	.05	.17	.71	.90	.12	.31
Tense	.34	.62	.44	.68	-.02	-.07	.42	.72	.57	.82
Timid	.54	.79	.45	.69	.39	.72	.11	.31	.47	.76
Trusting	.49	.75	.62	.81	.42	.74	.79	.93	.25	.53
Vigilant	-.01	-.04	.06	.16	.15	.41	.29	.59	-.02	-.09
Vocal	.34	.62	.33	.57	.58	.85	.37	.67	.55	.81
Mean	**.35**	**.58**	**.41**	**.59**	**.26**	**.52**	**.37**	**.61**	**.34**	**.58**

1. Agress.=Aggressive; Note: (c)=conspecifics; (p)=people

Clouded leopards

For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from .01 (reckless) to .80 (aggressive to people), with a mean reliability of .37. The reliabilities of mean ratings, ICC(3,*k*), ranged from .04 (reckless) to .93 (aggressive to people), with a mean reliability of .61. The ICCs for the items decisive, deliberate, fearful of conspecifics, persevering, quitting, and stingy were all negative, and so these items were excluded from further analysis.

For the subjective well-being items, the reliabilities of individual ratings, ICC(3,1), were .40 (ability to achieve goals), .61 (pleasure from social interactions with other clouded leopards), .62 (moods), .66 (be the clouded leopard), and .86 (pleasure from social interactions with people). The reliabilities of mean ratings, ICC(3,*k*), were .70 (ability to achieve goals), .85 (pleasure from social interactions with other clouded leopards), .85 (moods), .87 (be the clouded leopard), and .96 (pleasure from social interactions with people).

Snow leopards

For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from .02 (self-assured) to .64 (playful), with a mean reliability of .26. The reliabilities of mean ratings, ICC(3,*k*), ranged from .08 (self-assured) to .89 (playful), with a mean reliability of .52. The ICCs for the items persevering, smart, dominant, independent, quitting, aimless, tense, decisive, and bold were all negative, and so were excluded from further analysis.

For the subjective well-being items, the reliabilities of individual ratings, ICC(3,1), were .16 (pleasure from social interactions with people), .18 (ability to achieve goals), .21 (be the snow leopard), .51 (pleasure from social interactions with other snow leopards), and .51 (moods). The reliabilities of mean ratings, ICC(3,*k*), were .53 (pleasure from social interactions with people), .57 (ability to achieve

goals), .61 (be the snow leopard), .86 (pleasure from social interactions with other snow leopards), and .86 (moods).

African lions

For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from .04 (distractible) to .81 (submissive), with a mean reliability of .34. The reliabilities of mean ratings, ICC(3,*k*), ranged from .11 (distractible) to .94 (submissive), with a mean reliability of .58. The ICCs for the items predictable, impulsive, and vigilant were all negative, and so were excluded from further analysis.

For the subjective well-being items, the reliabilities of individual ratings, ICC(3,1), were .30 (be the lion), .36 (pleasure from social interactions), .37 (ability to achieve goals), and .37 (moods). The reliabilities of mean ratings, ICC(3,*k*), were .52 (be the cat) to .59 (pleasure from social interactions), .60 (ability to achieve goals), and .60 (moods).

Reliability comparison across species

Domestic cat ICC(3,1)s correlated with clouded leopard ($r=.55$, $p<.01$), Scottish wildcat ($r=.41$, $p<.01$), and snow leopard ($r=.55$, $p<.01$) reliabilities; Scottish wildcat ICC(3,1)s correlated with clouded leopard ICC(3,1)s ($r=.39$, $p<.01$); and clouded leopard ICC(3,1)s correlated with snow leopard ICC(3,1)s ($r=.41$, $p<.01$). African lion reliabilities did not correlate significantly with any other species; Scottish wildcat reliabilities did not correlate significantly with snow leopard reliabilities.

Taxon

For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from .03 (quitting) to .56 (playful), with a mean reliability of .32. The reliabilities of

mean ratings, ICC(3,*k*), ranged from .11 (quitting) to .83 (playful), with a mean reliability of .60.

For the subjective well-being items, the reliabilities of individual ratings, ICC(3,1), were .29 (ability to achieve goals), .40 (be the cat), .46 (pleasure from social interactions with conspecifics), .49 (moods), and .70 (pleasure from social interactions with people). The reliabilities of mean ratings, ICC(3,*k*), were .57 (ability to achieve goals), .68 (be the cat), .74 (pleasure from social interactions with conspecifics), .76 (moods), and .88 (pleasure from social interactions with people).

5.2 Principal components analysis

Scottish wildcats

For the personality data, principal components and parallel analysis, and examination of the scree plot indicated that three components accounting for 54.29% of the variance were described by the ratings. I compared the results of the principal components analysis and a regularised exploratory factor analysis by calculating Tucker's congruence coefficients (Wrigley & Neuhaus, 1955): ϕ=.994 for the first domain, ϕ=.993 for the second, and ϕ=.990 for the third. Values of .70 and above are considered to have mild agreement, .80 and above high agreement, and .90 and above equality (Sakamoto et al., 1998).

Based on the pattern of component loadings and previous research on trait groupings, I labelled the three components I found for Scottish wildcats Dominance (α=.93), Agreeableness (α=.90), and Self Control (α=.83) (Table 7). The reliabilities of individual ratings, ICC(3,1), were .68 for Dominance, .74 for Agreeableness, and .40 for Self Control. The reliabilities of mean ratings, ICC(3,*k*), were .85 for Dominance, .88 for Agreeableness, and .64 for Self Control.

For the well-being data, principal components and parallel analysis, and examination of the scree plot indicated that one component (α=.71) accounting for

Table 7 Scottish wildcat factor structures of mean trait ratings

	Principal-components analysis			Regularised exploratory factor analysis		
Item	Dominance	Agreeableness	Self-Control	Dominance	Agreeableness	Self-Control
Aggressive to people	**.88**	.08	-.05	**.64**	.11	.14
Dominant	**.87**	.21	.12	**.64**	.16	-.01
Bullying	**.83**	-.19	.30	**.52**	-.12	-.04
Stingy	**.82**	.32	.00	**.54**	.23	.03
Excitable	**.77**	.18	-.19	**.45**	.16	.16
Aggressive to conspecifics	**.74**	.28	-.35	**.50**	**.30**	.28
Impulsive	**.73**	-.16	-.31	**.39**	.00	**-.30**
Jealous	**.73**	-.11	.33	**.48**	-.10	-.10
Constrained	**-.72**	-.03	-.17	**-.46**	-.01	.04
Eccentric	**.72**	-.15	.11	**.46**	-.09	.02
Affectionate	**-.70**	.32	.31	**-.41**	.10	**.33**
Deliberate	**.56**	-.17	.34	-.28	-.10	-.08
Active	**.54**	.01	.36	**.35**	-.06	-.17
Vigilant	**.51**	.06	**-.50**	-.24	.15	**-.34**
Stable	**-.49**	.07	.14	**-.32**	.01	-.14
Friendly to conspecifics	**-.48**	.32	.25	.26	.10	-.26
Independent	**.41**	-.19	-.19	-.21	-.04	.19
Cooperative	.08	**.81**	.04	-.04	**.49**	-.16
Fearful of people	.15	**-.79**	-.24	-.08	**-.47**	**-.32**
Friendly to people	-.33	**.76**	-.02	.22	**.46**	-.15
Trusting	-.27	**.74**	**.41**	.15	**.40**	**.44**

Item	Principal-components analysis			Regularised exploratory factor analysis		
	Dominance	Agreeableness	Self-Control	Dominance	Agreeableness	Self-Control
Curious	.32	**.71**	-.12	-.17	**.44**	-.02
Playful	.03	**.68**	**-.50**	.04	**.47**	.17
Suspicious	.32	**-.68**	-.30	-.18	**-.36**	**-.39**
Insecure	-.07	**-.67**	**-.58**	.10	-.29	**-.42**
Timid	-.12	**-.66**	**-.57**	.14	**-.35**	**-.45**
Vocal	-.09	**.52**	-.27	.10	**.32**	.07
Fearful of conspecifics	.28	**-.49**	-.09	-.16	-.28	.18
Decisive	.27	-.09	**.82**	-.22	-.14	**.37**
Tense	.25	-.38	**-.78**	-.07	-.09	**-.56**
Self assured	.10	**.43**	**.60**	-.11	.16	**.39**
Solitary	.31	-.37	**-.60**	-.11	-.09	**-.44**
Aimless	.22	**.43**	**-.58**	-.05	.28	.23
Quitting	-.20	.06	**-.55**	.13	.10	.21
Cool	-.11	.14	**.55**	.00	-.01	**.33**
Calm	-.09	.25	**.52**	.00	.06	**.30**
Persevering	.36	-.03	**.49**	-.21	-.06	-.18
Predictable	-.09	-.08	**.46**	.01	-.10	-.25
Anxious	-.23	-.34	-.09	.16	-.18	.10
Erratic	.37	-.36	-.29	-.14	-.12	.22
Smart	.36	.21	.38	-.18	.07	-.15
Submissive	-.07	-.21	.01	.04	-.12	.02

Note: Salient loadings (>|.40| for PCA; >|.30| for REFA) are in boldface.

85.61% of the variance was described by the ratings. Three items had salient loadings (Table 8), so the fourth item (be the cat) was dropped from further analysis. The reliability of individual ratings, ICC(3,1), for subjective well-being was .32 and the reliability of mean ratings, ICC(3,*k*), was .55.

Domestic cats

Principal components and parallel analysis, and examination of the scree plot indicated that three components accounting for 53.19% of the variance were described by the ratings. I labelled the components I found for domestic cats Neuroticism (α=.96), Impulsiveness (α=.76), and Dominance (α=.86) (Table 9). The reliabilities of individual ratings, ICC(3,1), were .55 for Neuroticism, .42 for Impulsiveness, and .31 for Dominance. The reliabilities of mean ratings, ICC(3,*k*), were .79 for Neuroticism, .69 for Impulsiveness, and .58 for Dominance.

Clouded leopards

For the personality data, parallel analysis indicated that two components were described by the ratings, accounting for 59.65% of the variance, while examination of the scree plot indicated that there were three, accounting for 69.93% of the variance. A regularised exploratory factor analysis indicated three components as well. I compared the results of the three-factor solution principal components analysis with the regularised exploratory factor analyses: ϕ=.98 for the first domain, ϕ=.98 for the second, and ϕ=.98 for the third, implying equality.

Table 8 Factor loadings of Scottish wildcat subjective well-being items

Item	Loading
Balance of positive and negative moods	.92
Pleasure derived from social interactions	.91
Ability to achieve goals	.83
Be the wildcat	.09

Table 9 Domestic cat factor structure of mean trait ratings

Item	Neuroticism	Impulsiveness	Dominance
Anxious	**.89**	-.09	.06
Insecure	**.87**	-.21	-.11
Tense	**.87**	-.20	-.09
Stable	**-.86**	-.16	-.08
Affectionate	**-.86**	.06	-.00
Friendly to people	**-.85**	.00	-.29
Trusting	**-.84**	.02	-.11
Cool	**-.83**	-.08	.11
Calm	**-.82**	-.22	-.12
Suspicious	**.85**	.01	.13
Fearful of people	**.82**	-.24	.04
Timid	**.80**	-.24	-.18
Self-assured	**-.74**	.27	.06
Aggressive to people	**.73**	.08	**.45**
Cooperative	**-.72**	-.28	-.24
Curious	**-.53**	**.51**	.27
Constrained	**.53**	**-.47**	-.10
Excitable	.01	**.81**	.19
Active	-.34	**.72**	.07
Playful	**-.42**	**.66**	.18
Eccentric	.13	**.62**	.21
Impulsive	**.52**	**.56**	.08
Distractible	-.12	**.52**	.25
Reckless	**.40**	**.51**	**.45**
Independent	.08	**-.45**	.22
Aggressive to conspecifics	.37	.06	**.68**
Bullying	-.01	.07	**.63**
Submissive	-.06	-.02	**-.62**
Dominant	-.08	-.03	**.54**
Erratic	**.42**	**.44**	**.50**
Jealous	.08	**.41**	**.49**
Stingy	.19	.06	**.43**
Individualistic	.20	.31	**.42**
Persevering	-.03	.29	**.42**
Predictable	-.25	**-.42**	**.40**
Decisive	-.13	.02	.39
Vocal	-.16	.35	.26
Solitary	.08	-.29	.12
Fearful of conspecifics	.31	-.16	.08
Friendly to conspecifics	-.36	.22	-.30

Note: Salient loadings (>|.40|) are in boldface.

Because of these results, and based on the pattern of component loadings and previous research on trait groupings, I labelled the three components I found for clouded leopards Neuroticism (α=.95), Agreeableness/Openness (α=.93), and Dominance/ Impulsiveness (α=.89) (Table 10). The reliabilities of individual ratings, ICC(3,1), were .80 for Neuroticism, .90 for Agreeableness/Openness, and .47 for Dominance/ Impulsiveness. The reliabilities of mean ratings, ICC(3,*k*), were .93 for Neuroticism, .97 for Agreeableness/Openness, and .76 for Dominance/Impulsiveness.

For the well-being data, principal components and parallel analysis, and examination of the scree plot indicated that one component (α=.93) accounting for 83.81% of the variance was described by the ratings for all five items (Table 11). The reliability of individual ratings, ICC(3,1), for subjective well-being was .82 and the reliability of mean ratings, ICC(3,*k*), was .94.

Snow leopards

For the personality data, principal components and parallel analysis, and examination of the scree plot indicated that three components accounting for 71.06% of the variance were described by the ratings. I compared the results of the principal components analysis and a regularised exploratory factor analysis: ϕ=.97 for the first domain, ϕ=.97 for the second, and ϕ=.97 for the third, indicating equality.

Based on the pattern of component loadings and previous research on trait groupings, I labelled the three components I found for snow leopards Neuroticism (α=.94), Impulsiveness/Openness (α=.90), and Dominance (α=.92) (Table 12). The reliabilities of individual ratings, ICC(3,1), were .36 for Neuroticism, .44 for Dominance, and .71 for Impulsiveness/Openness. The reliabilities of mean ratings, ICC(3,*k*), were .70 for Neuroticism, .76 for Dominance, and .91 for Impulsiveness/Openness.

Table 10 Clouded leopard factor structures of mean trait ratings

Item	Principal-components analysis			Regularised exploratory factor analysis		
	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness
Self assured	**-.95**	-.14	-.00	**-.62**	-.07	.04
Insecure	**.91**	-.17	.06	**.59**	-.13	-.06
Fearful of people	**.89**	-.38	-.06	**.66**	**-.31**	.01
Cool	**-.88**	.28	-.28	**-.50**	.17	.20
Suspicious	**.86**	-.15	.34	**.60**	-.12	-.25
Calm	**-.85**	.13	-.34	**-.49**	.09	.22
Eccentric	**.79**	.24	.31	**.45**	.14	-.18
Solitary	**.78**	-.24	.01	**.42**	-.12	-.01
Trusting	**-.72**	**.54**	-.18	**-.51**	**.39**	.14
Tense	**.69**	-.34	**.47**	**.35**	-.18	-.27
Smart	**-.69**	.08	.26	-.22	.02	-.08
Stable	**-.61**	-.25	**-.61**	-.28	-.12	**.31**
Independent	**-.61**	**-.60**	-.06	-.28	-.28	.05
Vigilant	**.59**	.33	**.51**	.27	.15	-.26
Friendly to conspecifics	**-.57**	**.48**	.00	-.21	.19	.00
Anxious	**.52**	-.06	**.54**	.26	-.03	-.30
Distractible	-.06	**.93**	-.13	-.02	**.50**	.07
Playful	-.03	**.91**	.15	-.04	**.60**	-.12
Curious	.00	**.89**	-.03	.02	**.43**	.02
Affectionate	**-.45**	**.80**	-.02	-.27	**.49**	.03
Friendly to people	**-.52**	**.79**	.08	**-.41**	**.60**	-.05

Table 10 *continued*

Item	Principal-components analysis			Regularised exploratory factor analysis		
	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness
Cooperative	-.27	**.77**	.13	-.19	**.50**	-.08
Active	-.30	**.77**	**.50**	-.19	**.46**	-.29
Excitable	**.44**	**.67**	**.50**	.25	**.38**	-.28
Aggressive to people	**.46**	**-.62**	**.46**	**.34**	**-.43**	**-.31**
Vocal	**-.45**	**.55**	**.46**	**-.33**	**.41**	-.29
Timid	.23	**.51**	.05	.09	.22	-.01
Erratic	.17	.05	**.91**	.08	.02	**-.49**
Reckless	-.07	-.05	**.79**	-.05	-.03	**-.33**
Impulsive	.30	.37	**.79**	.16	.21	**-.48**
Aggressive to conspecifics	.34	-.31	**.73**	.14	-.14	**-.35**
Dominant	.02	.04	**.67**	.01	.03	-.29
Predictable	.32	-.37	**-.66**	.21	-.21	**.38**
Individualistic	.14	.07	**.59**	.07	.03	-.22
Submissive	-.35	.04	**-.54**	-.14	.02	.23
Constrained	.10	**-.41**	**-.53**	.03	-.12	.16
Bullying	.32	-.08	**.46**	.10	-.03	-.20
Jealous	-.02	.40	**.42**	.00	.20	-.24
Aimless	.35	.14	.21	.13	.06	-.05

Note: Salient loadings (>|.40| for PCA; >|.30| for REFA) are in boldface.

Table 11 Factor loadings of clouded leopard subjective well-being items

Item	Loading
Balance of positive and negative moods	.94
Pleasure derived from social interactions with other leopards	.83
Pleasure derived from social interactions with people	.95
Ability to achieve goals	.89
Be the clouded leopard	.97

For the well-being data, principal components and parallel analysis, and examination of the scree plot indicated that one component (α=.94) accounting for 83.64% of the variance was described by the ratings on all five items (Table 13). The reliability of individual ratings, ICC(3,1), for subjective well-being was .40 and the reliability of mean ratings, ICC(3,*k*), was .80.

African lions

For the personality data, principal components and parallel analysis, and examination of the scree plot indicated that three components accounting for 65.10% of the variance were described by the ratings. The Tucker's congruence coefficients between principal components analysis and the regularised exploratory factor analysis were ϕ=.99 for the first domain, ϕ=.94 for the second, and ϕ=.99 for the third.

Based on the pattern of component loadings and previous research on trait groupings, I labelled the three components I found for African lions Neuroticism (α=.96), Impulsiveness (α=.86), and Dominance (α=.86) (Table 14). The reliabilities of individual ratings, ICC(3,1), were .76 for Neuroticism, .55 for Impulsiveness, and .74 for Dominance. The reliabilities of mean ratings, ICC(3,*k*), were .92 for Neuroticism, .81 for Impulsiveness, and .91 for Dominance.

Table 12 Snow leopard factor structures of mean trait ratings

Item	Principal-components analysis			Regularised exploratory factor analysis		
	Neuroticism	Impulsiveness/ Openness	Dominance	Neuroticism	Impulsiveness/ Openness	Dominance
Trusting	**-.91**	.08	.01	**-.59**	.06	.01
Friendly to people	**-.86**	.18	.14	**-.59**	.13	.09
Suspicious	**.85**	-.10	**-.43**	**.44**	-.04	-.18
Fearful of people	**.83**	.02	-.38	**.58**	.00	-.25
Gentle	**-.82**	-.08	-.24	**-.39**	-.03	-.11
Affectionate	**-.80**	.18	-.26	**-.43**	.11	-.14
Aggressive to people	**.79**	-.16	.16	**.50**	-.13	.09
Cool	**-.72**	**-.53**	-.06	-.28	-.22	-.04
Stable	**-.66**	-.29	.05	-.28	-.10	.05
Calm	**-.65**	**-.53**	-.32	**-.33**	-.26	-.16
Individualistic	**.63**	-.27	-.09	.22	-.07	.03
Irritable	**.63**	-.25	.27	**.33**	-.13	.20
Timid	**.62**	.09	**-.58**	**.37**	.04	**-.33**
Anxious	**.60**	**.50**	.01	.22	.23	.06
Insecure	**.59**	.19	**-.52**	.26	.11	-.18
Distractible	**.54**	.31	**-.42**	**.31**	.11	-.26
Active	-.02	**.87**	-.15	-.01	**.42**	-.07
Curious	-.14	**.85**	-.20	-.06	**.38**	-.08
Inquisitive	-.30	**.83**	-.15	-.09	.27	-.07
Playful	.18	**.79**	**-.42**	.10	**.43**	-.21
Excitable	.10	**.76**	.17	.06	**.30**	.05

Item	Principal-components analysis			Regularised exploratory factor analysis		
	Neuroticism	Impulsiveness/ Openness	Dominance	Neuroticism	Impulsiveness/ Openness	Dominance
Inventive	-.25	**.74**	-.10	-.07	.22	-.05
Reckless	-.17	**.70**	**.46**	-.06	.25	.14
Impulsive	**.44**	**.69**	-.18	.16	.28	-.06
Clumsy	**-.47**	**.63**	.11	-.20	.28	.01
Eccentric	.08	**.61**	.00	.01	.28	.06
Bullying	.01	.02	**.87**	-.01	.03	**.42**
Stingy	.06	**.45**	**.82**	.03	.20	**.35**
Aggressive to conspecifics	-.05	-.24	**.82**	-.05	-.09	**.41**
Predictable	.22	-.34	**-.77**	.08	-.10	-.25
Friendly to conspecifics	-.19	.38	**-.75**	-.07	.15	**-.34**
Submissive	.17	.08	**-.70**	.09	.06	**-.33**
Solitary	-.11	**-.49**	**.70**	-.06	-.22	**.33**
Vocal	-.04	.10	**-.69**	.02	.02	**-.41**
Jealous	-.01	**.51**	**.67**	.02	.23	.29
Defiant	.36	-.08	**.64**	.12	-.01	**.32**
Erratic	.38	**.42**	**.62**	.13	.17	.25
Cooperative	.07	-.07	**-.60**	.01	.05	-.21
Constrained	-.12	-.31	**-.44**	-.07	-.05	-.10
Vigilant	-.04	**.44**	.24	-.04	.23	.17
Fearful of conspecifics	.34	.09	.09	.10	.07	.06
Deliberate	.29	-.18	-.12	.10	.01	.08
Self-assured	-.30	**-.43**	-.19	-.17	-.10	.02

Note: Salient loadings (>|.40| for PCA; >|.30| for REFA) are in boldface.

Table 13 Factor loadings of snow leopard subjective well-being items

Item	Loading
Balance of positive and negative moods	.96
Pleasure derived from social interactions with other leopards	.71
Pleasure derived from social interactions with people	.94
Ability to achieve goals	.97
Be the snow leopard	.97

For the well-being data, principal components and parallel analysis, and examination of the scree plot indicated that one component (α=.92) accounting for 81.53% of the variance was described by the ratings for all five items (Table 15). The reliability of individual ratings, ICC(3,1), for subjective well-being was .51 and the reliability of mean ratings, ICC(3,*k*), was .72.

Taxon

For the personality data, parallel analysis indicated five components (with a .0008 difference between eigenvalues for the fifth component); the scree plot indicated four. I therefore examined three factor structures, one with five components, one with four, and one with three, since the individual species each had three factors.

In each grouping, there were three clear components, which I labelled Neuroticism (α=.91), Dominance (α=.86), and Impulsiveness (α=.86). In the five-factor solution, the fourth factor had elements of Conscientiousness and, on the opposite end, Neuroticism. The fifth factor had four positive loadings: solitary, independent, individualistic, and vigilant, and two negative ones: affectionate and friendly to conspecifics. Most of the traits in the fourth factor of the five-factor solution loaded onto Dominance in the four-factor solution, with the exception of smart, which loaded onto Neuroticism. In the four-factor solution, the fourth factor had the same loadings as the fifth factor in the five-factor solution. Four of the six traits in this fourth factor were reassigned in the three-factor solution, and made sense as part of these factors.

Table 14 African lion factor structures of mean trait ratings

	Principal-components analysis			Regularised exploratory factor analysis		
Item	Neuroticism	Impulsiveness	Dominance	Neuroticism	Impulsiveness	Dominance
Fearful of people	**.88**	.01	-.14	**.49**	-.07	-.09
Insecure	**.84**	.42	-.20	**.65**	.16	-.12
Tense	**.84**	.47	-.16	**.61**	.19	-.08
Timid	**.84**	.20	-.24	**.57**	.04	-.14
Fearful of conspecifics	**.82**	.37	-.31	**.62**	.16	-.19
Deliberate	**-.80**	-.27	.27	**-.44**	-.04	.12
Constrained	**.79**	.35	-.31	**.48**	.10	-.15
Trusting	**-.79**	.13	-.21	**-.36**	.15	-.09
Self assured	**-.78**	**-.49**	.31	**-.62**	-.23	.18
Suspicious	**.74**	.04	-.28	**.39**	-.04	-.15
Anxious	**.72**	.65	-.16	**.59**	**.31**	-.06
Submissive	**.71**	.47	-.39	**.61**	.26	-.25
Persevering	**-.69**	.06	.35	**-.35**	.07	.20
Stable	**-.67**	**-.52**	-.07	**-.41**	-.16	-.07
Solitary	**.61**	-.01	-.50	**.43**	-.09	**-.33**
Calm	**-.60**	-.53	-.37	**-.41**	-.18	-.25
Affectionate	**-.59**	.22	-.22	-.27	.19	-.09
Decisive	**-.56**	-.28	.54	**-.34**	-.09	.26
Friendly to conspecifics	**-.55**	.07	-.22	-.23	.15	-.09
Smart	**-.52**	**-.51**	-.27	**-.35**	-.13	-.19
Dominant	**-.51**	**-.48**	**.63**	**-.49**	**-.33**	**.42**

Table 14 *continued*

Item	Principal-components analysis			Regularised exploratory factor analysis		
	Neuroticism	Impulsiveness	Dominance	Neuroticism	Impulsiveness	Dominance
Curious	**-.51**	.46	.07	-.21	**.32**	.06
Cool	**-.48**	-.44	.02	**-.35**	-.11	-.03
Aggressive to conspecifics	**-.43**	.05	**.74**	-.29	.05	**.47**
Active	-.03	**.77**	.00	.08	**.44**	.05
Erratic	.26	**.75**	.14	.25	**.32**	.14
Eccentric	-.19	**.75**	-.16	.01	**.33**	-.02
Distractible	.29	**.71**	-.25	.23	.26	-.07
Aimless	.11	**.70**	-.20	.15	.28	-.04
Excitable	.39	**.69**	-.31	.27	**.31**	-.11
Reckless	-.28	**.65**	.35	-.05	.26	.21
Playful	-.23	**.59**	-.37	-.04	**.46**	-.19
Independent	-.28	**-.57**	-.28	-.22	-.29	-.19
Vocal	-.29	**-.44**	.41	-.25	**-.31**	.23
Jealous	-.19	.00	**.82**	-.12	-.07	**.48**
Stingy	-.20	-.16	**.77**	-.19	-.21	**.53**
Aggressive to people	.11	.16	**.74**	.07	.06	**.48**
Bullying	-.36	-.28	**.74**	**-.32**	-.17	**.46**
Quitting	.55	.02	**-.66**	.29	-.06	**-.33**
Friendly to people	-.34	-.02	**-.56**	-.17	.05	-.30
Individualistic	-.05	.07	**-.42**	.01	-.01	-.21
Cooperative	-.09	-.12	.05	-.05	-.01	.01

Note: Salient loadings (>|.40| for PCA; >|.30| for REFA) are in boldface.

Table 15 Factor loadings of African lion subjective well-being items

Item	Loading
Balance of positive and negative moods	.96
Pleasure derived from social interactions with other lions	.71
Pleasure derived from social interactions with people	.94
Ability to achieve goals	.97
Be the lion	.97

Affectionate and friendly to conspecifics loaded on the negative end of Neuroticism, or Emotional Stability; solitary loaded on Neuroticism; and vigilant loaded on Dominance. Independent and individualistic were the only traits that dropped out from the salient loadings with this solution. Therefore, I used the three-factor solution for further analysis (Table 16).

The reliabilities of individual ratings, ICC(3,1), were .37 for Impulsiveness, .53 for Dominance, and .58 for Neuroticism. The reliabilities of mean ratings, ICC(3,*k*), were .69 for Impulsiveness, .81 for Dominance, and .84 for Neuroticism.

For the well-being data, principal components and parallel analysis, and examination of the scree plot indicated that one component (α=.90) accounting for 72.69% of the variance was described by the ratings for all five items (Table 17). The reliability of individual ratings, ICC(3,1), for subjective well-being was .67 and the reliability of mean ratings, ICC(3,*k*), was .87.

5.3 Correlations between personality and subjective well-being

Scottish wildcats

Subjective well-being was positively correlated with Self Control in results from both the principal components analysis (r=.67, p=.001) and the regularised exploratory factor analysis (r=.45, p=.04). Individually, Self Control was positively correlated with moods (r=.61, p=.004) and pleasure derived from social interactions (r=.69, p=.001) (Table 18). None of the other correlations were significant.

Table 16 Overall felid factor structure of mean trait ratings

Item	Neuroticism	Dominance	Impulsiveness
Trusting	**-.85**	.05	-.07
Fearful of people	**.80**	-.22	.01
Friendly to people	**-.76**	-.26	.16
Suspicious	**.75**	-.13	.28
Affectionate	**-.73**	-.32	.18
Insecure	**.67**	**-.56**	.26
Friendly to conspecifics	**-.67**	-.29	.05
Tense	**.66**	**-.44**	.34
Aggressive to people	**.60**	**.52**	.17
Cool	**-.60**	.25	**-.42**
Cooperative	**-.59**	-.06	.04
Playful	**-.58**	-.18	**.57**
Solitary	**.56**	-.08	-.10
Calm	**-.55**	.24	**-.48**
Anxious	**.54**	**-.48**	.32
Timid	**.54**	**-.57**	.14
Active	**-.51**	.08	**.60**
Self-assured	**-.49**	**.62**	-.35
Stable	**-.48**	.13	**-.50**
Fearful to conspecifics	**.41**	-.38	.12
Dominant	.05	**.78**	.06
Deliberate	.08	**.68**	-.27
Aggressive to conspecifics	.35	**.66**	.23
Stingy	.07	**.64**	.26
Decisive	-.14	**.64**	-.27
Persevering	-.17	**.61**	.13
Constrained	.24	**-.60**	-.14
Submissive	.07	**-.58**	.15
Bullying	.06	**.55**	.12
Jealous	-.02	**.47**	**.47**
Vigilant	.11	**.43**	.24
Impulsive	.16	.16	**.79**
Excitable	-.22	-.01	**.74**
Erratic	.28	.01	**.72**
Eccentric	.18	.12	**.70**
Reckless	.03	.13	**.67**
Distractible	-.16	-.06	**.59**
Aimless	.09	-.09	**.58**
Predictable	.50	.17	**-.56**
Individualistic	.20	.33	.38
Curious	-.38	.34	.33
Vocal	-.38	.18	.27
Quitting	.17	-.38	.09
Smart	-.23	.34	-.24
Independent	.13	.33	-.30

Note: Salient loadings (>|.40|) are in boldface.

Table 17 Factor loadings of overall felid subjective well-being items

Item	Loading
Balance of positive and negative moods	.95
Pleasure derived from social interactions with conspecifics	.78
Pleasure derived from social interactions with people	.72
Ability to achieve goals	.88
Be the felid	.91

Clouded leopards

Subjective well-being was negatively correlated with Neuroticism (r=-.79, p<.001) and positively with Agreeableness/Openness (r=.55, p=.027). Individually, Neuroticism was negatively correlated with moods (r=-.77, p<.001), pleasure derived from social interactions with other clouded leopards (r=-.81, p<.001) and with people (r=-.82, p<=.001), ability to achieve goals (r=-.77, p=.001), and be the clouded leopard (r=-.80, p<.001). Agreeableness/Openness was positively correlated with moods (r=.58, p=.018), pleasure derived from social interactions with people (r=.53, p=.034), and be the clouded leopard (r=.57, p=.021) (Table 19). None of the other correlations were significant.

Snow leopards

Subjective well-being was negatively correlated with Neuroticism in results from both the principal components analysis (r=-.67, p=.003) and the regularised exploratory factor analysis (r=-.67, p=.003). Individually, Neuroticism was negatively correlated with moods (r=-.50, p=.04) pleasure derived from social interactions with other snow leopards (r=-.60, p=.01) and with people (r=-.71, p=.001), and ability to achieve goals (r=-.62, p=.008). Impulsiveness/Openness was positively correlated with moods (r=.49, p=.048) and negatively with pleasure derived from social interactions with people (r=-.50, p=.043) (Table 20). None of the other correlations were significant.

Table 18 Scottish wildcat personality components and subjective well-being correlations (Spearman's rho)

Subject Well-Being	Factor (PCA)			Factor (REFA)		
	Dominance	Agreeableness	Self-Control	Dominance	Agreeableness	Self-Control
Overall	.03	.11	.67*	.10	-.10	.45**
Moods	.11	.24	.61*	.15	.03	.43**
Goals	.29	-.28	.34	.32	-.45**	.00
Pleasure from social interaction	-.19	.12	.69*	-.09	-.08	.55*

* Significant at the .05 level
** Significant at the .01 level

Table 19 Clouded leopard personality components and subjective well-being correlations (Spearman's rho)

Subject Well-Being	Factor (PCA)			Factor (REFA)		
	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness	Neuroticism	Agreeableness/ Openness	Dominance/ Impulsiveness
Overall	-.79**	.55*	-.05	-.77**	.59*	.03
Moods	-.77**	.58*	-.07	-.76**	.61*	.02
Pleasure from social interaction with conspecifics	-.81**	.13	-.21	-.76**	.18	-.21
Pleasure from social interaction with people	-.82**	.53*	-.05	-.79**	.57*	.02
Goals	-.77**	.32	-.03	-.71**	.36	.01
Be the cat	-.80**	.57*	-.11	-.77**	.61*	-.02

* Significant at the .05 level; ** Significant at the .01 level

Table 20 Snow leopard personality components and subjective well-being correlations (Spearman's rho)

Subject Well-Being	Factor (PCA)			Factor (REFA)		
	Neuroticism	Impulsiveness/ Openness	Dominance	Neuroticism	Impulsiveness/ Openness	Dominance
Overall	-.67**	.36	.20	-.67**	.31	-.03
Moods	-.50*	.49*	.28	-.52*	.42	.02
Pleasure from social interaction with conspecifics	-.60*	.26	-.06	-.60*	.28	-.23
Pleasure from social interaction with people	-.71**	.50*	.13	-.74**	.44	-.11
Goals	-.62**	.33	.30	-.59*	.24	.06
Be the cat	-.48	.45	.36	-.48	.38	.12

* Significant at the .05 level; ** Significant at the .01 level

Table 21 African lion personality components and subjective well-being correlations (Spearman's rho)

Subject Well-Being	Factor (PCA)			Factor (REFA)		
	Neuroticism	Impulsiveness	Dominance	Neuroticism	Impulsiveness	Dominance
Overall	-.66**	-.49*	.31	-.68**	-.39	.28
Moods	-.69**	-.34	.30	-.68**	-.23	.28
Pleasure from social interaction	-.27	-.51*	.00	-.32	-.50*	-.06
Goals	-.64**	-.60**	.41	-.69**	-.46*	.38
Be the cat	-.71**	-.43	.39	-.72**	-.34	.38

* Significant at the .05 level; ** Significant at the .01 level

African Lions

Subjective well-being was negatively correlated with Neuroticism (PCA: r=-.66, p=.001; REFA: r=-.68, p=.001) and with Impulsiveness (PCA: r=-.49, p=.02). Individually, Neuroticism was correlated with moods (r=-.69, p=.001), goals (r=-.64, p=.002), and be the lion (r=-.71, p<.001). Impulsiveness was correlated with pleasure derived from social situations (r=-.51, p=.019) and achieving goals (r=-.60, p=.004) (Table 21). None of the other correlations were significant.

Taxon

Subjective well-being did not correlate with any of the taxon factors. To better understand this result, which seemed counterintuitive, I conducted additional analyses, which involved calculating the correlations between the individual traits and subjective well-being in each species, and calculating the correlations between the individual traits and overall felid measure of subjective well-being. Six traits were correlated with subjective well-being across three species: affectionate (clouded leopards: r=.68, p=.004; snow leopards: r=.74, p=.001; lions: r=.45, p=.04), calm (clouded leopards: r=.58, p=.02; Scottish wildcats: r=.45, p=.04; lions: r=.60, p=.004), fearful of people (clouded leopards: r=-.93, p<.001; snow leopards: r=-.55, p=.02; lions: r=-.47, p=.03), suspicious (clouded leopards: r=-.66, p=.005; snow leopards: r=-.60, p=.01; lions: r=-.60, p=.004), tense (clouded leopards: r=-.76, p=.001, Scottish wildcats: r=-.60, p=.004; lions: r=-.74, p<.001) and trusting (clouded leopards: r=.78, p<.001; snow leopards: r=.64, p=.006; lions: r=.58, p=.006). Only insecure was the same across all four species (clouded leopards: r=-.75, p=.001; Scottish wildcats: r=-.65, p=.001; snow leopards: r=-.53, p=.03; lions: r=-.60, p=.004). Each species except Scottish wildcats had traits that correlated with subjective well-being only within the species. For clouded leopards, these were cool (r=.77, p=.001), cooperative (r=.58, p=.02), friendly to conspecifics (r=.73, p=.001), and smart (r=.52,

p=04). For African lions, they were constrained (r=-.50, p=.02), dominance (r=.52, p=.02), fearful of conspecifics (r=-.60, p=.004), persevering (r=.78, p<.001), stable (r=.54, p=.01), submissive (r=-.55, p=.01), and timid (r=-.53, p=.02). For snow leopards, these were individualistic (r=-.72, p=.001) and predictable (r=-.53, p=.03).

5.4 Age and sex effects

Scottish wildcats are rated as more Agreeable as they age (r=.56, p=.006); clouded leopards are rated as less Agreeable/Open (r=-.66, p=.006). Domestic cats (r=-.54, p<.001) and snow leopards (r=-.61, p=.009) are rated as less Impulsive as they age. There were no age effects in African lions.

Female African lions (M=.26, SD=.91) are rated as more Impulsive than males (M=-.83, SD=.88): t(19)=2.35, p=.03, d=1.22), but only when using the results from the regularised exploratory analysis. There were no sex effects in any of the other species.

5.5 Personality factor comparisons

To compare the five sets of factors, orthogonal targeted Procrustes rotation was used (McCrae et al., 1996). Congruence coefficients were calculated to compare the results (Table 22). Domestic cat factor Neuroticism was related to Scottish wildcat factor Dominance (ϕ=.89), clouded leopard Neuroticism (ϕ=.86), snow leopard Neuroticism (ϕ=.82), and lion factor Neuroticism (ϕ=.80), showing high agreement (Sakamoto et al., 1998). Scottish wildcat Dominance was related to snow leopard Neuroticism (ϕ=.70), showing moderate agreement (Sakamoto et al., 1998), and African lion Neuroticism (ϕ=.82). Clouded leopard Neuroticism was related to snow leopard Neuroticism (ϕ=.73), and African lion Neuroticism (ϕ=.71).

The domestic cat factor Impulsiveness was related to Scottish wildcat factor Agreeable (ϕ=.76), clouded leopard factor Agreeableness/Openness (ϕ=.75), snow

Table 22 Orthogonal Procrustes rotations among felid species personality factors

Species factors	Cat N	Cat I	Cat D	SWC D	SWC A	SWC SC	CL N	CL A/O	CL D/I	SL N	SL I/O	SL D
Cat N	xx	xx	xx									
Cat I	xx	xx	xx									
Cat D	xx	xx	xx									
SWC D	**.89**			xx	xx	xx						
SWC A		**.76**		xx	xx	xx						
SWC SC				xx	xx	xx						
CL N	**.86**				**.71**		xx	xx	xx			
CL A/O		**.75**				.64	xx	xx	xx			
CL D/I			.58	**.74**			xx	Xx	xx			
SL N	**.82**			**.70**			**.73**			xx	xx	xx
SL I/O		**.78**			**.70**			**.78**		xx	xx	xx
SL D			.51			.39			.57	xx	xx	xx
Lion N	**.80**			**.82**			**.71**			**.72**		
Lion I		**.71**			**.72**			.67			**.81**	
Lion D			.61			.65			.51			.32

Cat=domestic cat; SWC=Scottish wildcat; CL=clouded leopard; SL=snow leopard; Lion=African lion
N=Neuroticism; I=Impulsiveness; D=Dominance; A=Agreeable; O=Open; SC=Self Control
Note: .70 and above indicates moderate agreement; .80 and above indicates high agreement; .90 and above indicates equality

leopard Impulsiveness/Openness (ϕ=.78) and lion factor Impulsiveness (ϕ=.71). Scottish wildcat Agreeable was related to snow leopard Impulsiveness/Openness (ϕ=.70), and African lion Impulsiveness (ϕ=.72). Clouded leopard Agreeableness/ Openness was related to snow leopard Impulsiveness/Openness (ϕ=.78). Snow leopard Impulsiveness/Openness was related to lion Impulsiveness (ϕ=.81).

Only one relationship among the Dominance factors was found across species. Clouded leopard Dominance was related to Scottish wildcat Dominance (ϕ=.74).

Chapter 6

Discussion

Personality and subjective well-being ratings were reliable across raters for all species. The mean reliabilities of the dimensions showed clinical significance (Cicchetti, 1994), and all reliabilities showed similarities to those found in humans (Connolly, Kavanagh, & Viswesvaran, 2007; Gomà-i-Freixanet, 1997; Gomà-i-Freixanet, Wismeijer, & Valero, 2005; Pavot & Diener, 1993), and also in chimpanzees (Weiss et al., 2009), orangutans (Weiss et al., 2006), rhesus macaques (Weiss et al., 2011), and capuchin monkeys (Morton et al., 2013), all of which were measured using a similar instrument to that used in the current work. In addition, reliabilities were also similar to studies using different measures in a variety of species (Freeman & Gosling, 2010; Gosling, 2001; Jones & Gosling, 2005; Uher, Asendorpf, & Call, 2008).

A comparison of the reliabilities across species showed that most of the species' ICC(3,1)s correlated significantly, with the exception of African lions, and Scottish wildcats as compared with snow leopards. These results show that there is something different in the ratings for African lions, especially—perhaps due to the fact that they are the only purely social species among the felids. The highest reliabilities in lions, but not in any other species, were for the adjectives dominant and submissive, which reflect their social structure. The difference in Scottish wildcats and snow leopards is not apparent. The trait aggressive to people was one of the most reliable in snow leopards, clouded leopards, and domestic cats, but not Scottish wildcats, so perhaps this played a role in the difference found here. The most reliable Scottish wildcat traits included stable and predictable; it is possible that these traits, which did not show up in the top four most reliable traits in the

other species, caused enough of a difference with the snow leopards, while the similarities with other species overcame this difference.

6.1 Overview

The cat species studied had three personality factors, which were relatively consistent across species. Dominance, Neuroticism, and Impulsiveness bore similarities to similarly-labelled dimensions in other cat (cheetah [Wielebnowski, 1999] and snow leopard [Gartner & Powell, 2012]) and primate (chimpanzee [Weiss et al., 2009] and orangutan [Weiss et al., 2006]) species. In the following sections I will focus on the results from the PCAs, as they were shown to be equivalent to the REFA results, which were used to confirm the PCA results.

Neuroticism was related to lower subjective well-being in three of the four species (excepting Scottish wildcats, who did not have a Neuroticism factor), and in some cases other personality factors were related to subjective well-being as well (as described below). This is also the case in humans (Diener et al., 1999), chimpanzees (Weiss et al., 2009), orangutans (Weiss et al., 2006), and rhesus macaques (Weiss et al., 2011). For a trait-to-trait comparison across species included in this research, in addition to other research on big cats, non-human primates, and humans, see Table 23, which is modelled after a table from Weiss et al., 2011.

6.2 Scottish wildcat personality

Scottish wildcat personality ratings define three components. Dominance had the highest loadings on the traits aggressive to people, dominant, and bullying; Agreeableness had the highest loadings on the traits cooperative, (not) fearful of people, and friendly to people; and Self Control, which was related to higher subjective well-being, had the highest loadings on decisive, (not) tense, and self-assured. Self Control had elements related to low and high Conscientiousness in humans (decisive, persevering/quitting, aimless, predictable) (Digman, 1990).

Table 23 Comparison of domestic cat, Scottish wildcat, snow leopard, clouded leopard, and African lion personality domains with other species

	Current study					Other research[1]						
Item	Dom. cat	Scottish	Snow	Clouded	Lion	Cheetah[2]	Snow	Tiger	Orangutan[3]	Chimpanzee[3]	Macaque[3]	Human
Active	I+	D+	I/O+	A/O+	I+	VE+	AV+	E+	E+	E+	AC+	E+
Affectionate	N-	D-	N-	A/O+	N-				A+	E+	F+	A+
Aggressive/conspecifics	D+	D+	D+	D/I+	D+	A+		A+	D+	C-	D-	A-
Aggressive to people	N+	D+	N+	A/O-	D+	A+						
Aimless		SC-			I+							
Anxious	N+		N+	D/I+	N+		TA+		N+	D-	AN+	N+
Bold												
Bullying	D+	D+	D+	D/I+	D+				D+	D+	D+	A-
Calm	N-	SC+	N-	N-	N-	TF-	CSA+					
Clumsy			I/O+						I-	C-	AC-	C-
Constrained	N+	D-	D-	D/I-	N+							
Cool	N-	SC+	N-	N-	N-				N-	N-	AN-	N-
Cooperative	N-	A+	D-	A/O+			FH+					
Curious	I+	A+	I/O+	A/O+	N-	TF-	CP+	Y+	E+	O+	O+	O+
Decisive		SC+			N-				I+	D+	F+	C+
Defiant			D+						D+	C-	D+	A-
Deliberate		D+			N-							
Distractible	I+		N+	A/O+	I+					C-	CO-	C-
Dominant	D+	D+		D/I+	D+				D+	D+	D+	A-
Eccentric	I+	D+	I/O+	N+	I+	VE+	TA+					
Erratic	D+		N+	D/I+	I+				N+	C-	AN+	C-
Excitable	I+	D+	I/O+	A/O+	I+	VE+	TA+	Y+	N+	N+	D+	N+
Fearful of conspecifics		A-			N+	TF+			N+	D-	CO-	N+
Fearful of people	N+	A-	N+	N+	N+	TF+	TA+					
Friendly to conspecifics		D-	D-	N-	N-				A+	E+	F+	A+
Friendly to people	N-	A+	N-	A/O+	D-		FH+					
Gentle			N-						D-	A+	D-	A+
Impulsive	I+	D+	I/O+	D/I+				Y+	N+	C-	O+	E+
Independent	I-	D+		N-	I-				I+	D+	D+	N-
Individualistic	D+		N+	D/I+	D-					E-	D+	O+

Table 23 *continued*

	Current study					Other research[1]						
Item	Dom. cat	Scottish	Snow	Clouded	Lion	Cheetah[2]	Snow	Tiger	Orangutan[3]	Chimpanzee[3]	Macaque[3]	Human
Inquisitive			I/O+						E+	O+	O+	O+
Insecure	N+	A-	N+	N+	N+	TF+	TA+					
Inventive			I/O+						E+	O+	O+	O+
Irritable			N+						D+	C-	D+	A-
Jealous	D+	D+	D+	D/I+	D+				D+	C-	AN+	A-
Persevering	D+	SC+			N-				D+	D+	F+	C+
Playful	I+	A+	I/O+	A/O+	I+	VE+	CP+	Y+	E+	E+	AC+	E+
Predictable	D+	SC+	D-	D/I-					N-	C+	AC-	C+
Quitting		SC-			D-					C-	AN+	C-
Reckless	I+		I/O+	D/I+	I+				D+	C-	D+	C-
Self assured	N-	SC+	I/O-	N-	N-	TF-	CSA+					
Smart				N-	N-	VE+		A+	I+	D+	F+	O+
Solitary		SC-	D+	N	N+				E-	E-	F-	E-
Stable	N-	D-	N-	N-	N-				N-	N-	CO+	N-
Stingy	D+	D+	D+		D+				D+	D+	D+	A-
Submissive	D-		D-	D/I-	N+				D-	D-	CO-	A+
Suspicious	N+	A-	N+	N+	N+							
Tense	N+	SC-		N+	N+	TF+	TA+					
Timid	N+	A-	N+	A/O+	N+		TA+		N+	D-	CO-	E-
Trusting	N-	A+	N-	N-	N-		FH+					
Vigilant		D+	I/O+	N+			AV+	E+				
Vocal		A+	D-	A/O+	I-	VE+						

[1] Other research as follows: cheetah (Wielebnowski, 1999), snow leopard (Gartner & Powell, 2012), tiger (Phillips & Peck, 2007), orangutan (Weiss et al., 2006), chimpanzee (Weiss et al., 2009), rhesus macaque (Weiss et al., 2011), human (Goldberg, 1990; Costa & McCrae, 1992).

[1]Wielebnowski (1999) defined factor loadings ≥ |0.6| as salient. Because this study used ≥ |0.4| as a cutoff, I included those traits that fell within this rule as well.

[3]These studies used a very similar scale as the one used in the current study; research that is not footnoted used substantially different scales.

Key. Dom. cat=domestic cat; Scottish=Scottish wildcat; Snow=snow leopard; Clouded=clouded leopards; Lion=African lion; Macaque=rhesus macaque; Scottish wildcats: SC=Self Control; cheetahs: A=Aggressive, VE=Vocal/Excitable, TF=Tense/Fearful; snow leopards: AV=Active/Vigilant, CP=Curious/Playful, CSA=Calm/Self Assured, FH=Friendly to Humans, TA=Timid/Anxious; tiger: Y=Youthfulness; all other species: A=Agreeableness, C=Conscientiousness, D=Dominant, E=Extraversion, I=Impulsive, N=Neuroticism, O=Openness

Scottish wildcats were one of two species with an Agreeableness dimension. It was, however, moderately related to the other species' Impulsiveness factors. The traits on the negative end of Scottish wildcat Agreeableness were all related to Neuroticism; however, this factor did not show congruence with any of the other species' Neuroticism factors. The traits that were similar across Scottish wildcat Agreeableness and the Impulsiveness factors in other species are related to Extraversion and Openness, while the traits that loaded the highest on Scottish wildcat Agreeableness (cooperative, friendly, and trusting) are absent from Impulsiveness in the other species, but instead show up in the negative loadings of Neuroticism, as Emotional Stability. Some traits related to Openness, such as curious or playful, are often anecdotally associated with cats. It is not surprising then, that these traits loaded on factors across cat species. There are a number of possibilities that might explain the difference in how they manifest themselves in factors.

Anecdotally, Scottish wildcats are thought to be untameable. Similarly, their very close relative, the European wildcat, has been shown to exhibit fewer affiliative behaviours than other small felids (Cameron-Beaumont, Lowe, & Bradshaw, 2002). African wildcats, however, are thought to be more agreeable (Cameron-Beaumont et al., 2002); this is the basis of one theory as to why domestic cats evolved from that subspecies of wildcat, since tameability and attention-soliciting are considered to be pre-adaptations for domestication (Price, 2002). Similarly, instead of adaptations, these characteristics may have been incidental responses to the environment (Hare, Wobber, & Wrangham, 2012), which had one subspecies favouring affiliative individuals, while the other either did not, or favoured more aggressive individuals. Another possibility as to why Scottish wildcats have an Agreeableness factor is that they are not as untameable as believed, and are perhaps more like the African wildcat than previously thought. Assessing the personality of other species of wildcat, then, especially the African wildcat, would be instructive, as comparing

closely related species has the potential to reveal similarities and differences that may give hints as to how species characteristics either converged or diverged over time (Gosling & Graybeal, 2007).

In addition, as Scottish wildcats age, they are rated as more Agreeable—this is in line with results from other species, such as humans (McCrae et al., 1999) and chimpanzees (King et al., 2008).

6.3 Domestic cat personality

Domestic cat personality ratings define three components. Dominance had the highest loadings on the traits aggressive to conspecifics, bullying, and (not) submissive; Impulsiveness had the highest loadings on excitable, active, and playful—but traits that reflected Conscientiousness were more numerous, including eccentric, impulsive, distractible, and reckless. In addition, Cronbach's alpha was below .70 when playful was included, but above after its deletion. I named this factor based on findings in chimpanzees, which showed two facets to Conscientiousness: predictability, which included adjectives predictable, (not) impulsive, (not) reckless, (not) erratic, and (not) disorganised, and tameness, which included adjectives (not) defiant, (not) irritable, (not) aggressive, and (not) jealous (King et al., 2008). Neuroticism had the highest loadings on anxious, insecure, and tense.

As cats age, they become less Impulsive. Domestic cat Impulsiveness features some traits related to the social vitality aspect of Extraversion, which decreases in humans as they age during certain time periods (Roberts, Walton, & Viechtbauer, 2006). Similarly, other traits in this factor included elements on the Conscientiousness scale, and in humans, Conscientiousness increases with age (Roberts, Walton, & Bogg, 2005; Roberts et al., 2006), as it does in chimpanzees (King et al., 2008).

6.4 Clouded leopard personality

There were three components defined by the clouded leopard personality ratings, as interpreted via examination of a scree plot and regularised exploratory factor analysis. However, parallel analysis indicated two, so this research would benefit from replication and a larger sample size.

Neuroticism had the highest loadings on the traits (not) self assured, insecure, and fearful of people. Agreeableness/Openness had the highest loadings on distractible, playful, and curious, but had more loadings on traits related to Agreeableness. Finally, Dominance/Impulsiveness had the highest loadings on erratic, reckless, and impulsive, but had more loadings on traits related to Dominance.

The two-factor structure was comprised of Neuroticism/Impulsiveness and Agreeableness. The first had the highest loadings on the traits suspicious, eccentric, and vigilant, and the second on active, friendly to people, and affectionate. All traits related to Dominance/Impulsiveness in the three-factor structure loaded on Neuroticism/Impulsiveness except jealous, predictable, and constrained, which loaded on Agreeableness.

Unlike Scottish wildcats, age is negatively related to Agreeableness/Openness, which may reflect traits related to Openness more than others, as this factor tends to decrease with age in humans (McCrae et al., 1999) and chimpanzees (King et al., 2008).

6.5 Snow leopard personality

Snow leopard personality ratings define three components. Neuroticism had the highest loadings on the traits (not) trusting, (not) friendly to people, and suspicious; Impulsiveness/Openness had the highest loadings on active, curious, and inquisitive; and Dominance had the highest loadings on bullying, stingy, and aggressive to conspecifics. There were many more unreliable traits rated in snow

leopards than in the other cats. This may have been due to the fact that of the three participating zoos, one had only one rater, so had to be excluded from the reliability calculations.

Impulsiveness/Openness is negatively related to age. As mentioned above, Openness decreases as humans and chimpanzees age, as does Conscientiousness (McCrae et al., 1999). This result was only found in domestic cats and snow leopards, however, and would be an interesting aspect to pursue with larger sample sizes. Why doesn't lion Impulsiveness decrease with age? While lifespan across species is somewhat similar, my dataset of domestic cats, which were mostly urban strays or abandoned housecats, would generally live longer, and this may explain this result. Wild snow leopard longevity is uncertain.

6.6 African lion personality

African lion personality ratings define three components. Dominance had the highest loadings on the traits jealous, stingy, and aggressive to conspecifics; Impulsiveness had the highest loadings on the traits active, erratic, and eccentric; and Neuroticism had the highest loadings on fearful of people, insecure, and tense. Both Impulsiveness and Neuroticism were related to lower subjective well-being. African lions were the only species that showed a relationship between well-being and Impulsiveness. This may be because the snow leopard factor Impulsiveness/Openness was a mixed factor that included many elements of Openness. Scottish wildcats didn't have an Impulsiveness factor, and well-being measures weren't taken with domestic cats, who did have one. Impulsiveness was combined with Dominance in clouded leopards, which may explain the lack of a relationship in that species, as Dominance was not related to well-being in this dataset.

Female African lions were rated as more Impulsive than males. Aspects of Extraversion in this factor (active and playful) may play a role in this result. As

mainly females interact with their cubs, this may increase their ratings on this factor. Female lions are also directly affected by group living—the larger the pride, the more successful females are in reproducing, and the longer they live (Mosser & Packer, 2009). These elements of Extraversion, therefore, may play a role in group cohesion.

6.7 Relationships among personality factors

Domestic cat, lion, and snow leopard Neuroticism and Scottish wildcat Dominance are all inter-related to varying degrees. Scottish wildcats don't have a Neuroticism domain, and traits related to Neuroticism loaded on both Dominance and (negative) Agreeableness. While there is a moderate relationship between clouded leopard Neuroticism and Scottish wildcat Agreeableness, there is no relationship between the latter and domestic cat Neuroticism. Domestic cat Neuroticism is highly related to clouded leopard Neuroticism, however.

Scottish wildcat Agreeableness, along with domestic cat Impulsiveness, lion Impulsiveness, clouded leopard Agreeableness/Openness and snow leopard Impulsiveness/Openness are all inter-related, mostly moderately, with the snow leopard and lion factors being highly related. None of the Impulsiveness factors are very highly related, or equivalent.

Clouded leopard Dominance/Impulsiveness was similar to Scottish wildcat Dominance. This was the only relationship among the Dominance factors that were found in each species, which may indicate differences in how individuals interact across the species studied. The traits aggressive to conspecifics, bullying, and jealous loaded on all species' Dominance factors, while dominant loaded on all but snow leopards', and stingy loaded on all but clouded leopards'. Other than these traits, there was some variation among other traits that loaded both positively and negatively on the various species' Dominance factors, which may explain these

results. Research on behavioural indicators of Dominance may be of use in understanding these results.

These results suggest that the felid personality factors Neuroticism and Impulsiveness have not evolved too much since modern cats split off from Carnivora, although until genetic analyses are done this is uncertain. There is no obvious connection between either of these factors and adaptability, or to the felid's predatory way of life. It is possible that the results are related to the status of all the species in the study as captive animals, as contemporary evolution (Hendry & Kinnison, 1999) may play a role in the strengthening or weakening of traits (McDougall et al., 2006; see Chapter 7 for a more in-depth discussion of this topic). Unfortunately, it is nearly impossible to study personality in wild cats, as they are elusive (e.g., Nowell & Jackson, 1996). Studies have been done on groups of free-living domestic cats (e.g., Natoli et al., 2005), however they are limited to behavioural and not trait-based analyses. A possibility would be to look at animals kept in sanctuaries, such as lions in Africa; however, this would still present problems for the current methodology as the knowledge of the caretakers is probably much different than the knowledge of zookeepers, who spend more time in close proximity with the animals in their care. In addition, this approach was used in chimpanzees, but no difference in factor structure attributable to environment was found (King et al., 2005).

Because the snow leopard and lion are sister species (see Chapter 2), it makes sense that their personality structures would be similar, despite their different social structures. However, the fact that both the Scottish wildcat and domestic cat also have similar structures, as well as the clouded leopard, is more surprising. Domestication seems not to have played a role in the evolution of felid personality, and felid personality seems to be quite consistent. In terms of their role in their ecological niches, this makes sense. As predators, and obligate carnivores, cats, whether small or large, need to respond to similar challenges in the wild,

mainly having successful hunts, finding mates, and rearing young safely and effectively. Sociality seems not to play a role in personality evolution in felids, as the most social species (lions) had a similar personality structure to the least social (Scottish wildcats), but also semi-solitary (domestic cats) species. This is not the case in apes, where orangutans, a semi-solitary species, show differences in personality to chimpanzees, for example. However, chimpanzees and orangutans diverged eight million years apart (Locke et al., 2011), whereas lions and cats are only separated by about four million years (Johnson et al., 2006), which may account for the similarity in the latter, and the differences in the former.

However, none of the personality structures were identical, nor were there any with very high agreement. These differences may in fact indicate that there is some sort of evolutionary difference to be found, but that it exists at the facet level.

6.8 Taxon personality

The combined personality ratings of the five species also define three components. Neuroticism had the highest loadings on the traits fearful of people, suspicious, and insecure; Dominance had the highest loadings on the traits dominant, deliberate, and aggressive to conspecifics; and Impulsiveness had the highest loadings on impulsive, excitable, and erratic. This type of information could be useful for practical situations, for instance in zoos, where time is at a premium. Because there does seem to be a consistent personality structure across the taxon, one survey could be used, facilitating the process of personality assessment, saving time and energy, and increasing sample sizes (Watters & Powell, 2012). Before that could be done, however, personality in more species in the taxon would need to be assessed.

Interestingly, none of these overall taxon factors were related to well-being. The differences in the relationship between facets and well-being in each species offers some clues as to why this may be. Only one adjective, insecure, was associated with well-being in all four species. Affectionate (all but Scottish wildcats);

calm (all but snow leopards); and fearful of people, suspicious, and trusting (all but Scottish wildcats) were associated with well-being in three species each. Facets that correlated with well-being in Scottish wildcats and clouded leopards included active and solitary. Decisive correlated with well-being in Scottish wildcats and African lions. Clouded leopard facets that correlated with subjective well-being—cool, cooperative, friendly to conspecifics, and smart—indicate that positive interactions are especially important for their well-being, including those within their social structure (friendly to conspecifics), but also with others (e.g., cooperative). African lion facets—constrained, dominance, fearful of conspecifics, persevering, stable, submissive, and timid—seem to indicate that for this species, elements of their social structure are important for their well-being. Snow leopards only had two adjectives that correlated with well-being only in their species: individualistic and predictable. Overall, these results hint at species differences in well-being, despite personality similarities.

6.9 Personality factors in terms of other animals

Using a different survey, Wielebnowski (1999) also found three factors of personality in cheetahs: Tense-Fearful (with high positive loadings on tense, fear of conspecifics, fear of people, and insecure, and high negative loadings on self-assured, curious, and calm); Vocal-Excitable (comprised of vocal, excitable, playful, active, smart, and aggressive to people), and Aggressive (aggressive to people and to conspecifics).

With another survey, based partly on Wielebnowski's (1999), Phillips and Peck (2007) also labelled a three-factor solution for tiger personality, which included Extraversion, Agreeableness, and Youthfulness. Extraversion was comprised of skittish, oblivious, vigilant, and active; Agreeableness included careless, aggressive, focus, intelligent, and obedient; and Youthfulness included playful, excitable, impulsive, and curious.

Although the labels are different, there are clear similarities across species, even using different versions of trait-based surveys. The Tense-Fearful factor in cheetahs may relate to the Neuroticism factor in the five species I studied. Vocal-Excitable in cheetahs and Extraversion in tigers might be similar to the Impulsiveness factor in the present study, and Aggressive in cheetahs might be similar to Dominance. It would be worth using the same method on all species in order to conduct a direct comparison, especially in cheetahs, as they are separate from the Panthera line, which encompassed all of the big cat species in this study.

6.10 Well-being

Reliabilities for subjective well-being were similar to those found in primates such as orangutans (Weiss et al., 2006), chimpanzees (Weiss et al., 2009), and rhesus macaques (Weiss et al., 2011).

There have been no other studies using this scale for well-being in cat species. But there are some similarities in the relationship between personality and well-being found in cat species and that found in primates. The negative association between well-being and Neuroticism in snow leopards, clouded leopards, and lions is not surprising, as it replicates results in humans—Neuroticism is the strongest predictor of low well-being in humans (Steel et al., 2008)—and other primates (chimpanzees: Weiss et al., 2009; orangutans: Weiss et al., 2006; rhesus macaque Anxiety: Weiss et al., 2011; squirrel monkeys [*Saimiri boliviensis*]: Wilson, pers. comm.). Neuroticism is known to have a negative impact on health outcomes, from immunology to morbidity to mortality (Capitanio, 2011; Deary et al., 2010;), so it makes sense that that result can be found in primates, who are closely related to humans, but also in cats, who share genetic homologs with humans (Pontius et al., 2007).

In snow leopards, the item pleasure derived from social interactions with other leopards loaded slightly lower than the other items. This is probably due to

the fact that a few keepers left this blank, possibly because they had not witnessed the snow leopard interacting with other snow leopards. Interestingly, although Impulsiveness/Openness did not correlate with subjective well-being overall, two items did correlate, but in different directions. While the item moods was positively associated with Impulsiveness/Openness, pleasure derived from social interactions with people was negatively correlated with this personality factor. This may be an artefact of the small sample size. Alternatively, it could be that the relationship between the item moods and well-being was reflecting the Openness aspect of the factor, as has been found in other species. The relationship between the social interactions item and well-being may reflect differences in how species react to their caretakers—for example, in clouded leopards, the relationship seems to improve their well-being. Perhaps snow leopards are less fitted to coping with the social aspect of the captive environment.

In lions, well-being is negatively related to Impulsiveness. This is also a predictable result, as its opposite, Conscientiousness, is known to impart protective aspects for human health (Deary et al., 2010) and is positively related to well-being in humans. Similarly, Scottish wildcat Self Control, positively related to well-being, has elements of Conscientiousness and also negative Neuroticism. (The very low loading for the be the wildcat item for Scottish wildcat well-being is most likely due to the omission of ratings for this item from most of the keepers at one zoo.) Interestingly, the item goals was significantly related to Scottish wildcat Agreeableness in the REFA, but not in the PCA. Agreeableness was not related to overall subjective well-being, however. The only item that loaded on Agreeable in the REFA and not the PCA was aggressive to conspecifics, which had a very low loading (.30). The items that loaded in the PCA and not the REFA were insecure, fearful of conspecifics, self assured and aimless. It's possible that the difference among these traits played a role in this discrepancy. For example, it's possible that insecure and fearful do not describe the negative end of Agreeableness as accurately

as they could, and therefore do not relate to ratings of achieving goals in the well-being assessment.

Finally, clouded leopard Agreeableness/Openness is positively related to well-being—again, this is unsurprising, as related factors in other species have a similar relationship to well-being (humans: Steel et al., 2008, DeNeve & Cooper, 1998; chimpanzees: Weiss et al., 2009; orangutans: Weiss et al., 2006; rhesus macaque Friendliness: Weiss et al., 2011). Because Agreeableness was not related to well-being in Scottish wildcats, it is possible that the facets related to Openness were the ones driving the relationship in clouded leopards. In humans (Steel et al., 2008) and chimpanzees (Weiss et al., 2009), Openness is related to well-being (as is Agreeableness), but it isn't in macaques (Weiss et al., 2011; orangutans don't have an Openness factor: Weiss et al., 2006).

6.11 Methodological Variation

In addition to the method employed in this thesis, there are other ways that non-human animal personality can be measured. Considering that this science is still relatively new, this makes sense, and as yet there is no agreement on the best methodology. Two other methods that are employed include the behavioural repertoire approach (Uher, 2008) and qualitative behavioural analysis (QBA; Wemelsfelder et al., 2001).

The behavioural repertoire approach

The behavioural repertoire approach requires the definition of a set of species-specific behaviours, which are identified with descriptions of observable, measurable behaviours (Uher, 2008). These behaviours are then grouped by similarity non-empirically (if necessary to reduce complexity), and then factor analysed to form trait domains. While this bottom-up approach has been shown to

be both reliable and valid (Uher & Asendorpf, 2008), it is not without its limitations. Most importantly for this work, this method is not useful in comparative research, as it's designed to be species specific (Weiss & Adams, 2008). Other criticisms include the lack of systematic categorisation of behaviours (one behaviour being categorised as a motor vs. a social behaviour, for example; Carere & Maestripieri, 2008), the difficulty of identifying universal species-specific behaviours (for example, self-biting due to abnormal rearing, or behaviours resulting from brain damage; Carere & Maestripieri, 2008; Realo & Allik, 2008), and the idea that behaviour must only be defined as that which occurs in reaction to situation stimuli (Carere & Maestripieri, 2008).

Qualitative behavioural analysis

Another behaviourally based method, qualitative behavioural analysis assesses the "whole animal" (Wemelsfelder et al., 2001). That is, the method qualitatively assesses the expressive style of an animal's behaviour in the context of its environment at the current state of assessment. Participants observe animals and generate their own terminology of behaviour—free choice profiling—based on those observations. They then rate the animals' behaviour on a scale based on their own list of behaviours, which are reduced into principal dimensions. While the method uses personality terminology, it extends its use to assess a current state of welfare through behaviour. This method has shown high inter-observer reliability, repeatability, and observer detection of individual differences (Wemelsfelder et al., 2001), and has been validated with correlations to physical parameters (Rutherford et al., 2012; Stockman et al., 2011, Wickham et al., 2012). However, it is aimed more at an overall welfare assessment within a specific context than an understanding of just personality itself.

6.12 Methodological Disputes

Anthropomorphic projection or phylogenetic continuity?

Non-human personality researchers are often faced with charges of anthropomorphism (the attribution of human affects to non-humans [Rivas & Burghardt, 2002]); specifically that it is difficult for humans to rate animals reliably without imposing our views, or ourselves, onto them (e.g., Bolhuis & Wynne, 2009; Réale et al., 2007; Rose, 2007). There are many arguments that refute this claim. First, traits and personality factors have been shown with statistics to be rated reliably across raters, species, zoos, and even cultures (Gosling & Vazire, 2002; e.g., King, et al., 2005). These ratings show similar reliability estimates as those found in humans, with interobserver agreement correlations around .50 in humans and .52 in a summary of 21 studies of non-human animals (Gosling & Vazire, 2002). Indeed, Vazire et al. (2007) showed that the trait rating method is not only reliable, but more reliable than other methods such as behavioural coding. Looking at the reliability of both trait ratings and behavioural coding in the same study, the authors found that reliability was substantially higher in trait ratings, and that where there wasn't convergence between the two methods, the disparity was due to unreliable behavioural coding. If raters were using anthropomorphism—consciously or not—to rate animals, reliability would, by definition, be poor. The charge that raters may talk to each other, and therefore get an agreement on personality before rating each animal, thereby affecting reliability, has been shown to be moot both in humans (Funder et al., 1995) and in non-human animals (Vazire et al., 2007).

In addition, when asked to come up with their own list of traits, independent observers still show agreement in personality descriptions (Wemelsfelder et al., 2001), and indeed come up with similar traits that are often used in trait rating research. Those traits, as mentioned earlier, correlate with such physical parameters as core body temperature, heart rate, plasma glucose, and the neutrophil: lymphocyte ratio in cattle, as well as experience vs. naïveté of road

transport (Stockman et al., 2011); and heart rate, heart rate variability, and core body temperature in sheep (Wickham et al., 2012), as well as experience vs. naïveté of road transport. Similarly, an association was found between traits defined with this method and the before-and-after results of a drug known to decrease aggression and stress in pigs (Rutherford et al., 2012). Similar physical parallels to personality are found in humans (e.g., Caplan & Jones, 1975; Colquhoun, 1984).

Second, if, for the sake of argument, we are imposing our humanness onto animals, we do so no more strongly than we do with other humans. For example, Kwan et al. (2008) showed that human projections onto dogs are no stronger than those onto other humans. Therefore if one accepts that we can measure personality in humans without bias (e.g., Costa & McCrae, 1992; John, et al., 2007), and this is usually accepted based on the literature, then the same can be said for measuring it in non-human animals.

Third, if the results of animal personality research are simply anthropomorphic projections, one would expect to see similar personality structures across species, including humans (Gosling & John, 1999). But this is not the case, even among primates. In fact, our closest relative, the chimpanzee, shows some differences in personality structure from humans (Weiss et al., 2009).

Fourth, Weiss et al. (2012) directly address the issue of anthropomorphic projections by measuring rater-based effects and their relationship to personality ratings in chimpanzees and orangutans. The authors first removed rater effects from their analysis, and found similar personality factors as were originally found. They then removed animal effects (that is, the variability in animal traits), and found different factors. Finally they carried out a multilevel exploratory factor analysis that showed high congruence between animal-based loadings and unadjusted loadings in both species. This indicates that anthropomorphism was not occurring in these ratings.

Fifth, if personality research just reflected an anthropomorphic viewpoint, one would not expect to find heritability in personality factors in non-human species. However, the chimpanzee personality factor Dominance shows significant narrow-sense heritability (i.e., variance due to additive genetic effects, or that caused by differences among genes, not interactions between genes; Weiss et al., 2000), while variation in orangutan personality is explained mostly by nonadditive effects (Adams et al., 2012).

Finally, and perhaps most importantly, there have been arguments that anthropomorphism in and of itself is not a bad thing, and might be a good, or even necessary, thing (Burghardt, 1991; de Waal, 2009; Rivas & Burghardt, 2002). As long as the above holds true, that is, that the scientific method is being used, and that reliability isn't compromised, using anthropomorphism as a tool does not necessarily lead to bad science, or useless information as some contend (e.g., Bolhuis & Wynne, 2009). For instance, Burghardt argues that critical anthropomorphism (1991) is not only a good way to look at animal behaviour, but that without it, bad science may emerge. Critical anthropomorphism allows the researcher to take into account various inputs, including perceptions but also behaviour, to form ideas that allow understanding of a problem, as well as enables novel scientific predictions.

Without anthropomorphism, mistakes due to anthropodenial (de Waal, 2009) or anthropomorphism by omission (Rivas & Burghardt, 2002) may compromise the research. By avoiding any theory that is based on relating our experiences to non-human animals, we omit important information about that animal. For example, play behaviour is extremely hard to define (Fagen, 1981; Mitchell, 1990, Burghardt, 2005), and there is no fast agreement on a definition. However, we can sometimes recognise play in ourselves as in other species—for instance, when two kittens wrestle or chase one another, acts that, in and of themselves, would not automatically be defined as play. It would be an error to describe playful behaviour as simply a sum of its parts: wrestling, chasing,

bouncing, running, and jumping, etc. (Not to argue that to scientifically research play we don't need a definition—we do [Burghardt, 2005]). In so doing, we miss out on a behaviour that we see across species. If our goal is to understand species as well as we can, leaving out such a behaviour would impair our understanding of, in this case, several species. And yet, our recognition of play is based on identifying intent (de Waal, 2000) that we have experienced ourselves. So using our knowledge of human interaction, in this case, actually helps us to better understand animal behaviour.

Behavioural observations vs. trait ratings

A related contention is that trait ratings in animal personality research are too subjective (Vazire et al., 2007). However, as mentioned above, trait rating is not only more reliable, it's also less subjective than behavioural coding (Vazire et al., 2007), which is often held up as the objective method. From creating an ethogram to categorising behaviours to coding behaviours, behavioural coding is not only not objective, it's quite subjective (Vazire et al., 2007; Block, Weiss, & Thorne, 1979). Indeed, some consider it a fallacy to describe behavioural observations as objective (Bakeman & Gottman, 1986, in de Waal, 2000). Trait ratings, on the other hand, which are based on an aggregate of behaviours over many contexts and time, are less so. This misconception has led to a bias in behavioural coding use, as opposed to, and not in conjunction with, trait ratings. It is arguable, therefore, that trait ratings are the best way of measuring animal personality, either alone, or together with behavioural coding.

Claims that subjective well-being and personality are the same construct

Subjective well-being has been said to lack independence when it is measured by the same raters who assess personality in the same sample. While on the surface this

may seem like a valid argument, there are several factors that show that this is not the case. First, subjective well-being is comprised of three overall concepts: affect, which is related to personality as mentioned earlier in terms of negative and positive affect and Neuroticism and Extraversion, respectively; life satisfaction; and domain satisfactions as described earlier. So personality does not completely describe well-being, as life circumstances can influence long-term well-being (DeNever & Cooper, 1998; Diener, 1996; Diener, Oishi, & Lucas, 2003). Second, if subjective well-being were measuring the same thing as personality, the correlation between the two constructs would be expected to be higher than it is. However, this is neither the case in this work, nor in others using the same measure (e.g., Weiss et al., 2006). Third, in humans, Extraversion accounts for 19% of the variance in positive affect, while Neuroticism accounts for 29% of the variance in negative affect (Steel et al., 2008). Twin studies have shown that genetic influences in subjective well-being account for about 44 to 52 percent of the variance (Lykken & Tellegen, 1996). While all the heritable variance of well-being is shared with personality variance in humans (Weiss et al., 2002) and chimpanzees (Weiss et al., 2008), there are still remaining non-shared environmental effects (Lykken & Tellegen, 1996), which may not be common to personality and subjective well-being. For example, in chimpanzees, different non-shared environmental effects affect subjective well-being and Dominance, which are affected by the same genes (Weiss et al., 2002); maternal effects were also shown to influence subjective well-being in this species. In addition, while there is no phenotypic correlation between Dominance and subjective well-being in orangutans, there is one on the genetic level (the animal and rater covariances went in opposite directions and cancelled out), showing that raters are not unduly rating well-being and personality in the same way (Adams et al., 2012).

Sample size

Although in the past it was commonly held that sample sizes had to be at a minimum of at least 200, or based on a set ratio between sample size and number of cases (de Winter, Dodou, & Wieringa, 2009), recent work has suggested that that is not necessarily the case (e.g., Jung & Lee, 2011; de Winter et al., 2009). It is rare to have large sample sizes when studying captive animals, and especially big cats in captivity, or domestic cats in shelters. Therefore, I found it necessary to address the issue with the statistics used in this work to minimise any possible effects. In addition to measuring reliability and using parallel analysis, regularised exploratory analysis, designed specifically for smaller sample sizes, was used. This methodology works for sample sizes smaller than 50 (Jung & Lee, 2011), and offered similar results to the principal components analysis, without changing the overall factors.

In addition, the domestic cat sample included 100 animals. It is unlikely that the factors in this species would be related to factors in the other species, as shown through the Procrustes analysis, if those factor structures were not valid.

Chapter 7

The Importance of Personality Research in Non-Human Animals: Applications

There is considerable research on personality applications in humans, especially in terms of health outcomes, from immune function (Sutin et al., 2010) to morbidity (Goodwin & Friedman, 2006), mortality (e.g., Booth-Kewley & Friedman, 1987; Pedersen & Denollet, 2006; Jonassaint et al., 2007), and well-being (Diener et al., 1999). It makes sense then, that similar outcomes may be found in other mammals, considering phylogenetic continuity. (Indeed it wouldn't be surprising to find similar outcomes in other non-human animals as well; however, research in that area is minimal.) And this does seem to be the case—similar results have been found in other primates, from the relationship between personality and disease and disease contraction, to mortality, immune functioning, stress, and well-being. And, in terms of the latter, my research has shown similarities in felid species as well. Because a large percentage of these species are vulnerable or endangered, this type of research has the potential to make a critical difference in conservation efforts, of which zoo management is a part.

7.1 Health outcomes

Immune function

In humans, high Neuroticism and low Conscientiousness are associated with higher levels of interleukin-6 and C-reactive protein, markers of chronic inflammation (Sutin et al., 2010). Immune function is also associated with personality in non-human animals.

In non-human primates, experimental studies of rhesus (Capitanio et al., 2008; Capitanio, Mendoza, & Baroncelli, 1999) and cynomolgus monkeys (*Macaca fascicularis*, Kaplan et al., 1991) show that the personality factor Sociability has a

protective role in relation to the immune system, similarly to humans (Ironson et al., 2008). Rhesus monkeys higher in Sociability exposed to social stress experience an increase in antibodies in response to inoculation with simian immunodeficiency virus (SIV), while those lower in Sociability had a decrease in antibodies. In addition to the negative effects of the virus itself and the resulting acquired immune deficiency syndrome (AIDS), an inability to fight an infection (e.g., cytomegalovirus) following SIV infection can negatively affect longevity. However, Capitanio et al. (2008) found that low Sociability is only detrimental to health if animals are in unstable, unfamiliar conditions.

Similarly, cynomolgus monkeys both high in affiliation and low in aggression exposed to social stress show a healthier immune response, with a greater proliferation of lymphocytes (a type of white blood cell) in response to stimulation with mitogens (a chemical substance that causes cells to divide; this is a common way of testing immune function), and greater natural killer (NK) cytolytic activity (cells that kill virally infected cells) (Kaplan et al., 1991; see also Cohen et al., 1992).

In pigtailed (*Macaca nemestrina*) and bonnet (*Macaca radiata*) macaques, the personality factor Emotional Reactivity in response to a stressor may compromise immunity. In one experiment, monkeys were separated from their mothers; those that vocalised more on the first day of separation had less proliferation of white cells two weeks later in response to mitogens (Laudenslager et al., 1990). Similar results were found in rhesus monkeys (Laudenslager et al., 1993).

Morbidity

Immune function is not the only way that personality affects morbidity. In humans, high Conscientiousness and Extraversion and low Neuroticism are associated with reduced risk of such mental disorders as depression, panic attacks, generalised anxiety disorder, and substance abuse; high Conscientiousness is also associated

with reduced risk of such physical disorders as diabetes, high blood pressure, and sciatica, among others (Goodwin & Friedman, 2006).

A link has also been found between personality and disease contraction in domestic cats. Natoli et al. (2005) analysed temperament, social rank, and prevalence of feline immunodeficiency virus (FIV), a lethal disease that is transmitted by biting (Fromont et al., 1997), in three cat colonies in Rome and Lyon. Focal animal sampling was used to record six behavioural categories: aggressive, submissive, affiliative, territorial, display, and mating behaviours. When subjected to principal components analysis, the categories revealed one clear bipolar factor, proactive-reactive. Proactive included the most aggressive and affiliative males who marked (spraying or rubbing cheeks) frequently. Reactive described submissive individuals who were rarely aggressive. Proactive males had the highest social rank, and were the oldest, largest, and heaviest animals. Blood sampling of the male cats (who have higher rates of FIV infection than females) revealed that most infected males were high ranking and proactive. Proactive males had increased reproductive success, but they also had increased chances of being infected with FIV.

The opposite result is found in domestic cats with feline leukaemia virus (FeLV), which is transmitted mainly during affiliative interactions including licking and grooming (Fromont et al., 1997). More aggressive cats, then, have lower levels of FeLV, while socially active cats have higher levels (Fromont et al., 1997).

This link between personality and morbidity can be found in other species as well. Female Sprague–Dawley rats (*Rattus norvegicus*) labelled as neophobic, or less exploratory, had significantly more risk of developing spontaneous mammary and pituitary tumours than neophilic, or more exploratory females, and therefore increased mortality—they died six months earlier (Cavigelli et al., 2006). In addition, Kavelaars et al. (1999) found that aggressive wild-type rats were more susceptible to experimental autoimmune encephalomyelitis (an animal model of brain inflammation) than nonaggressive rats, and that the result was not due to

differences in hypothalamic-pituitary-adrenal (HPA) axis activity. This is unsurprising, as aggression bears similarities to toxic characteristics of type A personality in humans, which is characterised by, among other things, antagonistic hostility (related to lower Agreeableness and moderately related to higher Neuroticism: Dembroski & Costa, 1987), and which may play some role in coronary heart disease (Booth-Kewley & Friedman, 1987).

Stress

Stress, which can be measured by HPA activity (Tsigos & Chrousos, 2002) and is related to disease susceptibility, is also related to personality. In humans, Neuroticism can influence increases in anxiety (Bolger, 1990). Similarly, Wielebnowski et al. (2002) found that clouded leopards rated as more fearful/tense, and who self injured, paced, slept, and hid more often, had increased overall, base, and peak fecal corticoid concentrations, indicating chronic stress.

A relationship between personality and stress is found in non-human primates as well. Rhesus macaques rated as higher in Excitability had lower basal cortisol concentrations (during one phase—blood taken at 13:00 h—of the two-phase experiment) and those rated as higher in Confidence had higher cortisol concentrations (Capitanio, Mendoza, & Bentson, 2004). Tufted capuchins (*Cebus apella*) showed positive and negative correlations between personality traits strong and submissive, respectively, with baseline cortisol; and between apprehensive, fearful, insecure, and tense and confident, curious, effective, and opportunistic, respectively, with peak cortisol (Byrne & Suomi, 2002).

There is some evidence that personality interacts with behavioural reactions to stress as well. Solitary, irritable, and aggressive Diana monkeys (*Cercopithecus diana*) demonstrate increased abnormal behaviour during high visitor density, while active, playful, and excitable monkeys show an increase in species-typical behaviours, including play (Barlow et al., 2006). Sapolsky (1994) found that certain

behavioural styles were associated with lower basal cortisol concentrations, including those that allow the animal to differentiate threatening and neutral situations, those in which the animal is the initiator of aggression, those that dictate how the animal behaves after either winning or losing a battle with a rival where winners display affiliative behaviour and losers display displacement behaviour, and where the preceding three traits are correlated.

Similarly, a review of the relationship between personality and cortisol in birds found that for those species studied (great tits [*Parus major*], Japanese quail [*Coturnix coturnix japonica*], and hens [*Gallus gallus domesticus*]), those with proactive personalities had lower corticosterone stress responses to stimuli than those with reactive personalities (Cockrem, 2007).

Mortality

Personality has also been shown to predict mortality in a variety of species, including humans; both Conscientiousness and Extraversion seem to be protective and influence longevity, while Neuroticism has an unclear effect (Roberts et al., 2007). Examples in other species include male neophobic Sprague–Dawley rats, which were 60 percent more likely to die at any point in time than neophilic rats, with a 20 percent decrease in overall lifespan (despite dying of the same causes: tumours or urinary tract blockage; Cavigelli & McClintock, 2003). In western lowland gorillas (*Gorilla gorilla gorilla*), the personality dimension Extraversion predicted longer survival as assessed over 18 years, and regardless of demographic information such as age or sex or husbandry practices such as number of transfers among zoos (Weiss et al., 2013).

Well-being

Personality is also one of the strongest and most consistent predictors of well-being in humans (Diener et al., 1999) and non-human primates (e.g. King & Landau, 2003),

especially in relation to Extraversion and Neuroticism. In chimpanzees, King and Landau (2003) found that subjective well-being was related to higher Dominance, Extraversion, and Dependability. Weiss et al. (2009) replicated those results, but also found a positive relationship between subjective well-being and Agreeableness and Openness and a negative one with Neuroticism. In addition, orangutan personality—specifically Extraversion, Agreeableness and low Neuroticism—is also related to subjective well-being (Weiss et al., 2006). Finally, a similar relationship is found in rhesus macaques, where higher Confidence and Friendliness and lower Anxiety are related to subjective well-being (Weiss et al., 2011).

This is important not only as happiness is generally considered a good state in which to be at any moment, but also because subjective well-being is associated with longer life in humans (Diener & Chan, 2011) and orangutans (Weiss, Adams, & King, 2011). As such, well-being may be a good marker for health outcomes, as personality may be influencing health via subjective well-being. For example, in cynomolgus monkeys, depression, a facet of the unpleasant affect aspect of subjective well-being, mirrors that in humans in terms of physiology, neurobiology, and behaviour, including increased cardiovascular disease risk, increased mortality, and more, and is subject to individual differences in terms of response to environmental challenges (Willard & Shively, 2012).

According to Deary et al. (2010), there are four major applications of personality to health care and the improved well-being of humans: heightened surveillance for those with traits related to earlier mortality; the development of specific, individual intervention strategies; targeted drug treatments; and improved relationships between patients and health-care practitioners. These can be translated into care for captive animals. For instance, both Wielebnowksi (1999) and Carlstead et al. (1999) suggested that a better relationship between an animal and its keeper should improve welfare. This relationship could affect the remaining applications. Once relationships between personality and mortality in non-human animals are

established, keepers could attend differently to individuals with personality profiles related to risk, especially in terms of behavioural abnormalities. Similarly, individual interventions could be based on this increased awareness, and grouping, enrichment and medical interventions could, where appropriate, all be tailored to certain personalities. While zoo animals are not typically given drug treatments that address issues related to prevention of stress or personality, this might be an area for further research. Each of these areas contributes to the overall welfare of an animal, since each works to decrease specific causes of stress. While some have suggested that personality factors have implications for increasing welfare directly (for example, Wielebnowski, 1999), more work is needed. This should be an important next step in furthering the literature on personality and welfare.

7.2 Zoo management

Welfare

Environmental enrichment, which is comprised of additions to captive animal enclosures that encourage natural behaviour (Chamove, 1989), is a common tool in captive management. It has been shown to be effective at reducing stereotypic behaviour, which is characterised by aimless, invariant, repetitive actions (Shyne, 2006). However, abnormal behaviour remains common, even with efforts aimed to reduce it (e.g., in clouded leopards: Wielebnowski et al., 2002, and in chimpanzees: Birkett & Newton-Fisher, 2011), so different approaches are needed.

There is little work done on the direct effect personality may have on captive animal welfare. One study found that chimpanzees rated as higher in Openness were more interested than other chimpanzees in cognitive enrichment in the form of mirror recognition and touchscreen tasks (Herrelko, Vick, & Buchanan-Smith, 2012). The studies mentioned above in the Stress section are applicable here

(Wielebnowski et al., 2002; Capitanio et al., 2004; Byrne & Suomi, 2002; Barlow et al., 2006; Sapolsky, 1994; Cockrem, 2007).

Several researchers have made suggestions as to possible links between personality and welfare, including the ideas that shy or fearful animals may need more places to hide (snow leopards: Gartner & Powell, 2012; cheetahs: Wielebnowski, 1999), or that an animal's physical behaviour may need further explanation, which may lead to better understanding of welfare. For example, if a sheep is alert and active, is it also calm, or is it fearful (Wemelsfelder, 2007a)? How that animal is handled would be dependent on the latter assessment, and without knowledge of both the species and the individual, that animal's welfare could be impacted. For instance, in a study of farm pigs, veterinary inspectors were asked to score pig body language after observing the pigs for 10 minutes (Wemelsfelder, 2007b). While the inspectors were used to rating pigs as healthy or unhealthy, the study offered them a tool to understand the whole animal (Wemelsfelder et al., 2001; as described in Chapter 6). The inspectors showed agreement in their assessments, and saw a change in behaviour among pigs housed in various conditions, from intensive indoor to extensive outdoor facilities. That is, a physically healthy pig could nevertheless be frustrated or unhappy based on housing conditions. By qualitatively rating an animal's behavioural style, an inspector could more accurately describe the pig's welfare. This result allowed the inspectors to discuss the situation with the farmers they were dealing with and to try to improve the animal's welfare.

Using qualitative behavioural assessment, three studies have found links between the results of the assessment and other welfare measures. For instance, thoroughbred horse yearlings rated as suspicious/nervous or impatient/reactive before handling were consequently rated as more explorative/sociable and calm/apathetic (Minero et al., 2009). In another study using this method, pigs housed on extensive farms were rated as more happy and lively than those housed

in intensive conditions (Temple et al., 2011). Another study on calves found that signs of cross-sucking, an abnormal behaviour, were related to higher levels of activity and liveliness as described by the QBA, and animals rated as more fearful and agitated were found more often on farms with daily visits from an unfamiliar person (a technician or veterinarian) (Brscic et al., 2009).

Captive breeding

To help conserve species, zoos are often called upon to orchestrate captive breeding efforts (Wielebnowski, 1998). These efforts require careful consideration of spatial needs, species and individual behaviour, as well as genetic differentiation to avoid inbreeding. While some species breed well in captivity, others have more trouble, due a variety of problems, including aggression (Wielebnowski et al., 2002), disinterest (Powell et al., 2008), or poor health and/or stress (Clubb & Mason, 2003). Several methods have been used to increase the likelihood of successful breeding, including species- or, ideally, individual-specific environmental enrichment and providing an appropriate social environment (Shepherdson, 1994), to varying effect. In the past decade, research has emerged that has shown that in some species at least, personality can influence how animals interact in captive breeding situations. Because this is the case, personality should be taken into account when conducting captive breeding programs.

For example, Wielebnowski (1999) found that cheetahs rated as Tense-Fearful were more likely to be non-breeders ($U=93$, $p<.001$). While female cheetahs scored higher on the dimension than males overall, non-breeding cheetahs of both sexes scored higher on that dimension than successful breeders.

Carlstead et al. (1999) found that the most successful breeding occurred when dominant female black rhinoceros (*Diceros bicornis*) were paired with submissive males ($r=.75$, $p<.0001$), and that this was the most important behavioural predictor of successful breeding among the factors the authors assessed.

Similarly, Powell et al. (2008) found that high scores on shyness in female giant pandas (*Ailuropoda melanoleuca*) were correlated with poorer socio-sexual performance, while bold, confident females were less likely to be aggressive to males, and more likely to show interest in them. The authors suggested that bold males may have increased socio-sexual performance.

These studies show that taking personality into account when assessing breeding pairs in captive situations has the potential to increase successful breeding, but also to increase welfare by decreasing the stress of unsuccessful pairings, which can sometimes lead to attacks on potential mates in some species, for example, clouded leopards (Wielebnowski et al., 2002).

Enclosure grouping

In captive situations, enclosure groupings may change due to new additions to the zoo population to increase genetic diversity (Powell, 2010). There is some evidence that personality may play a role in how well captive animals respond to new overall groupings, or a new addition (Barlow et al., 2006; Gold & Maple, 1994; Powell, 2010; Stoinski et al., 2004). For example, bachelor gorilla (*Gorilla beringei beringei*) groups formed with silverbacks that were two standard deviations above the mean for the personality factor Understanding were successfully maintained (Stoinski et al., 2004), whereas usually it is very difficult to introduce an older male into an established group successfully. In other cases, these types of groups are the most successful when the group is comprised only of young animals. Introducing a new silverback to an established group of females can also be aided by knowing the personality of the animals involved. Successful introductions are more likely to occur if an aggressive silverback is introduced to dominant females first; or a timid or submissive male is introduced to subordinate females first (Powell, 2010).

In addition, taking personality into account in where an introduction takes place may increase the success of the introduction. When new animals are being

introduced to timid or submissive animals, a more successful outcome occurs in the cage of the more timid animal (Powell, 2010). This is often the case with felids, where males are more likely to be aggressive during an introduction, therefore the meeting is recommended to take place in the female's enclosure (Andrews, 1998). It is likely, then, that taking this outcome a step further to address each individual's personality would only increase successful introductions. This also applies to captive breeding.

Captive felids are often kept in multi-animal enclosures. Despite common knowledge that cat species are mostly solitary, excluding lions, it is becoming more established that some species, such as domestic cats, tigers, cheetahs, and lynx, are semi-solitary, forming social groups in certain situations, often related to food availability, but also family relationships (dispersing sibling groups, long-term parental care; Kitchener, 2000). It makes sense, then, that there is some evidence that social interaction may decrease abnormal behaviours and increase natural behaviours in pair-grouped captive tigers, for example (De Rouck et al., 2005). Knowing each animal's personality could potentially increase grouping success. For instance, tigers housed near other tigers show an increase in stereotypic behaviour. Because, as noted earlier, personality is linked to stress, taking personality into consideration when choosing which tigers to house near one another may decrease these behaviours.

7.3 Conservation

Reintroduction and translocation are two commonly used conservation methods for endangered species (Powell & Gartner, 2012); however, these programs are often unsuccessful (Beck et al., 1994; Fischer & Lindenmayer, 2000). This may be due to a variety of reasons, including the hypotheses that animals may not be used to predators, and therefore may fail to be vigilant enough, to avoid them, or to even recognise them (Griffin et al., 2000; in wallabies: Short et al., 1992; in golden lion

tamarins: Beck et al., 1991; and in African wild dogs: Frantzen, Ferguson, & de Villiers, 2001); may not be trained to forage for themselves or may not have enough genetic diversity (Frantzen et al., 2001); may not be establishing viable populations (Wolf et al., 1996); or may have trouble adapting to a new site (in prairie dogs: Truett et al., 2001; Kleiman, 1989).

A few studies have shown that taking personality into account may increase the success rate of these programs. For example, Bremner-Harrison et al. (2004) found that cautious swift foxes (*Vulpes velox*) were more successful in release scenarios than bold ones. Foxes that died within six months of release were all described as bold. Foxes assessed as bold by novel object tests were shown to travel further after release, and the authors suggested that they were less likely to avoid predators, conspecifics, or other potential risks.

Because individuals often have different survival strategies, and different personality types may have evolved within this framework, releasing just one personality type is not recommended. Watters and Meehan (2007) argue that mixing behavioural type is good for reintroduction, since individuals of one type may be good at one thing—like predation, for example—while another may be good at another thing—like vigilance. A mixed group, therefore, may be more able to cope with a new environment. Sih and Watters (2005) found that a mix of behavioural types can affect both individual and group fitness. They found that behavioural type in a group of water striders affected both the group outcome—a group with only low activity/aggression males led to the creation of a hyper-aggressive male, which inhibited mating in the group—and individual outcomes—the hyper-aggressive males were less likely to mate.

In terms of translocation, some species fare better when moved with members of their family. For example, black-tailed prairie dogs (*Cynomys ludovicianus*) are five times more likely to survive with family groups than alone (Shier, 2006), mainly due to predation. It is possible that this result may be due to

personality similarities within families. But social species are not the only ones who seem to benefit from group familiarity in translocation. Stephens' kangaroo rats (*Dipodomys stephensi*) that were translocated with neighbours had higher survival and reproductive rates than those translocated with unfamiliar animals (Shier & Swaisgood, 2009). The authors suggest that behaviour following release is indicative of the success of the neighbour groups: they fought less, and spent significantly more time foraging and burrowing. Is familiarity with a neighbour or family related to the interplay of personality within the group? Considering the results of reintroduction research, personality should also be observed in translocation work.

7.4 Evolution

Personality is related to fitness, as mentioned above, including mortality and fecundity. While many understand the implications for wild animals, those for captive animals are not often taken into account.

Captive breeding, for example, may have unforeseen consequences for fitness (McDougall et al., 2006). If animals are not being released to the wild, this may not represent a problem. Some species are so endangered that whether it's a problem or not, there is little choice but to carry out captive breeding. However, if reintroduction is an option, several problems may arise. For example, animals that are more active or more aggressive fare less well in captivity (McDougall et al., 2006), and these traits may start to decrease in frequency in captivity. But in some species, these traits may offer survival strategies that are more successful than others. Other pressures on selection that may occur in captivity include the novel environment, the retention of traits that have been selected against in the wild due to relaxed natural selection, and unconscious artificial selection due to husbandry practices (McDougall et al., 2006). Importantly, captive-reared animals have a much lower success rate than wild-caught animals in both reintroduction and translocation programs (Griffith et al., 1989).

Chapter 8

Conclusions and Future Studies

This work has shown that both personality and subjective well-being can reliably be assessed in cat species, and that some personality factors are related to subjective well-being in these species, similarly to primates including humans.

All five of the cat species studied, which ranged from the basal species of Panthera to the most newly evolved domestic cat, showed three factors of personality, mostly similar, suggesting that these factors developed in a common ancestor.

This information has the potential to be very useful for both captive management and conservation efforts, which is especially important for cat species, most of which are endangered. From increasing welfare to more successful captive breeding and reintroductions, personality, an underutilised tool in this field, can have far reaching effects that require a large amount of research that has yet to be done. As in humans, these results suggest a targeted, individual approach to care.

It would be interesting to assess species in other felid lineages, as personality is not wholly genetic, but also based on developmental and environmental events. Does the three-factor model hold across the taxon? If it does, the obvious next step would be to look at other closely related taxa—canidae, ursidae, phocidae, equidae, rhinocerotidae—when did that personality structure change?

Another line of inquiry would be a comparison between wolves and dogs. Originally I had expected to find an effect of domestication on the personality of domestic cats as compared to the Scottish wildcat, but I found nothing conclusive. Did domestication play a role in dog personality? If yes, why in dogs and not (necessarily) in cats? Does canid personality have the same relation to well-being as

felid personality does? Longitudinal work, which is lacking in many species, would be helpful.

Most personality work is aimed at mammals, or, in behavioural ecology, insects and fish. What about dolphins? Commonly thought to be the smartest animal on earth next to humans, is their personality similar as well? Is there a relationship to a colloquially defined species personality (dolphins are friendly, otters are playful) and their actual personality structure?

In addition to studying animal personality, studying its relationship to health outcomes should be a priority. Is there a direct link between personality and welfare? Does personality affect longevity in other species than gorillas? And, of course, there is a wealth of research that could be done in genetics and personality and subjective well-being both in felids and other species.

Finally, comparative studies of animals in the wild with captive animals could be revealing. This would be very difficult with cat species, as they are mostly elusive. But a beginning could be made with lions, or with other cats in a middle ground area such as a sanctuary. Are there differences among these groups?

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Appendix

Personality survey

I am a doctoral student at the University of Edinburgh, conducting a study on [insert species name] personality. I would like you to share your observations of the behavior of each particular animal so that I can compare it to other [species name]. There are no right or wrong answers. I am interested in your impressions, therefore, please do not consult with other keepers on your answers.

For each behavioral characteristic below, you'll see a ranking scale for that characteristic. Please circle a ranking along that continuum, indicating how strongly you think each snow leopard demonstrates that characteristic. Below, you'll see a list of all of the personality characteristics and their definitions. Some of them are similar to one another, and their definition may differ from your idea of what the words mean. Please try to answer the questions using the definitions provided here. You should also consider how the animal is *in general* with regard to that characteristic as opposed to remembering particular incidents.

If you have trouble judging a characteristic confidently, leave it blank, but please try to answer as many as you can.

Definitions
Active: Moves frequently (e.g., paces, runs, stalks often)
Affectionate: Warm attachment or closeness with other snow leopards or with people. This may include grooming, touching, or lying next to other snow leopards, or being responsive to humans.
Aggressive to conspecifics: Reacts in a hostile way or attempts to attack/threaten other snow leopards
Aggressive to people: Reacts in a hostile way or attempts to attack/threaten people
Aimless: Without any clear purpose or direction
Anxious: Interested but fearful and uneasy; vacillates between approach and withdrawal
Bold: Daring, not restrained or tentative
Bullying: Overbearing and intimidating towards others
Calm: Not easily disturbed by changes in the environment
Clumsy: Subject is relatively awkward or uncoordinated during movements including but not limited to walking and play

Constrained: Controlled and limited
Cool: Unaffected by emotions and usually undisturbed, assured, and calm
Cooperative: Is compliant; willingly behaves when asked to do something
Curious: Seeks out or investigates novel situations
Decisive: Deliberate, determined, and purposeful in its activities
Defiant: Assertive or contentious in a way inconsistent with the usual dominance order. Maintains these actions despite unfavorable consequences
Deliberate: Intentional, planning
Distractible: Easily distracted and has a short attention span
Dominant: Controlling, exerting forcefulness, powerful
Eccentric: Shows stereotypic or unusual behaviors
Erratic: Inconsistent, indefinite, and widely varying in behavior and moods
Excitable: Overreacts to changes in the environment
Fearful of conspecifics: Retreats readily from other snow leopards
Fearful of people: Retreats readily from people
Friendly to conspecifics: Initiates proximity with other snow leopards; approaches other snow leopards readily and in a friendly manner (purrs, rubs)
Friendly to people: Initiates proximity; approaches fence readily and in a friendly manner (e.g., purrs, rubs on fence)
Gentle: Subject responds to others in an easy-going manner. Subject is not rough or threatening.
Impulsive: Displays spontaneous or sudden behavior that was not anticipated
Independent: Behavior not influenced or controlled by other animals, events, or things
Individualistic: Behavior stands out compared to that of other individuals
Inquisitive: Subject seems drawn to new situations, objects, or animals. Subject behaves as if it wishes to learn more about others or objects within its view.
Insecure: Seems scared easily, jumpy and fearful in general
Inventive: Subject is more likely than others to do new things including novel behaviors.
Irritable: Often seems in a bad mood, or is impatient and easily provoked to anger or exasperation and consequent agnostic behavior
Jealous: Often troubled by others who are in a desirable or advantageous situation such as having food, a choice location, or access to social situations. May attempt to disrupt activities of advantaged snow leopards
Persevering: Continues in a course of action, task, or strategy for a long time or continues despite opposition
Playful: Initiates and engages in play behavior (seemingly meaningless, but non-aggressive behavior) with objects
Predictable: Consistent and steady behavior over extended periods of time. Does little that is unexpected or deviates from its usual behavioral routine
Quitting: Subject readily stops or gives up activities that have recently been started
Reckless: Rash or unconcerned about the consequences of its behaviors
Self-assured: Moves in a seemingly confident, well-coordinated, and relaxed manner
Smart: Snow leopard is quick and accurate in judging and comprehending situations. Learns quickly to associate events and appears to remember for a long time.
Solitary: Spends time alone; avoids company
Stable: Reacts to environment in a calm, equable, way
Stingy/Greedy: Excessively desirous or covetous of food, favored locations, or other resources. Unwilling to share these resources with others
Submissive: Often gives in or yields
Suspicious: Not trusting; does not approach easily
Tense: Shows restraint in movement and posture

Timid/shy: Reluctance to approach other animals, novel objects or new situations
Trusting: Not suspicious; approaches easily
Vigilant: Watchful, observant; spends a lot of time attending to its surroundings
Vocal: Frequently and readily vocalizes

Name of cat	***not at all***						***very much so***
Constrained	1	2	3	4	5	6	7
Vigilant	1	2	3	4	5	6	7
Stable	1	2	3	4	5	6	7
Bold	1	2	3	4	5	6	7
Clumsy	1	2	3	4	5	6	7
Defiant	1	2	3	4	5	6	7
Gentle	1	2	3	4	5	6	7
Inquisitive	1	2	3	4	5	6	7
Inventive	1	2	3	4	5	6	7
Irritable	1	2	3	4	5	6	7
Distractible	1	2	3	4	5	6	7
Erratic	1	2	3	4	5	6	7
Solitary	1	2	3	4	5	6	7
Impulsive	1	2	3	4	5	6	7
Quitting	1	2	3	4	5	6	7
Independent	1	2	3	4	5	6	7
Smart	1	2	3	4	5	6	7
Jealous	1	2	3	4	5	6	7
Fearful of conspecifics	1	2	3	4	5	6	7
Persevering	1	2	3	4	5	6	7
Stingy/Greedy	1	2	3	4	5	6	7
Friendly to conspecifics	1	2	3	4	5	6	7
Submissive	1	2	3	4	5	6	7
Dominant	1	2	3	4	5	6	7
Reckless	1	2	3	4	5	6	7
Predictable	1	2	3	4	5	6	7
Suspicious	1	2	3	4	5	6	7
Individualistic	1	2	3	4	5	6	7
Affectionate	1	2	3	4	5	6	7
Insecure	1	2	3	4	5	6	7
Bullying	1	2	3	4	5	6	7

Curious	1	2	3	4	5	6	7
Aimless	1	2	3	4	5	6	7
Deliberate	1	2	3	4	5	6	7
Tense	1	2	3	4	5	6	7
Fearful of people	1	2	3	4	5	6	7
Cool	1	2	3	4	5	6	7
Aggressive to people	1	2	3	4	5	6	7
Calm	1	2	3	4	5	6	7
Aggressive to conspecifics	1	2	3	4	5	6	7
Excitable	1	2	3	4	5	6	7
Friendly to people	1	2	3	4	5	6	7
Playful	1	2	3	4	5	6	7
Vocal	1	2	3	4	5	6	7
Decisive	1	2	3	4	5	6	7
Self-assured	1	2	3	4	5	6	7
Anxious	1	2	3	4	5	6	7
Trusting	1	2	3	4	5	6	7
Active	1	2	3	4	5	6	7
Cooperative	1	2	3	4	5	6	7
Timid/shy	1	2	3	4	5	6	7
Eccentric	1	2	3	4	5	6	7

Keeper Information

1. Name _____ Sex: M__ F__

2. How many months/years have you worked with

Name of cat _____

3. How well do you know

	not well						*very well*
Name of cat	1	2	3	4	5	6	7

4. How many days per week are you responsible for the care of these animals?_____

5. How many hours per day do you spend with them where you can see each other?_____

6. How many hours per week are you able to spend just watching these animals?

_____

THANK YOU VERY MUCH FOR YOUR TIME AND COOPERATION!

Well-being survey

This questionnaire has five questions relating to the subjective well-being of the *[species name]* at your zoo. Each question asks about a different personality dimension relating to subjective well-being. The following scale should be used to make your ratings.

1. Displays either total absence or negligible amounts of the trait or state.
2. Displays small amounts of the trait on infrequent occasions.
3. Displays somewhat less than average amounts of the trait.
4. Displays about average amounts of the trait.
5. Displays somewhat greater than average amounts of the trait.
6. Displays considerable amounts of the trait on frequent occasions.
7. Displays extremely large amounts of the trait.

Please give a rating for each item even if your judgment seems to be based on a purely subjective impression of the snow leopard and you are somewhat unsure about it. Indicate your rating by circling the chosen number. Please do not discuss your ratings with anyone else. This restriction is necessary in order to obtain valid reliability coefficients for the traits.

Date (Day/Month/Yr): Rater's full name:
Snow leopard name:
How long have you known the snow leopard (in years, months, days)?

1. Estimate the amount of time the snow leopard is happy, contented, enjoying itself, or otherwise in a positive mood. Assume that at other times the snow leopard is unhappy, bored, frightened, or otherwise in a negative mood.

least most
1 2 3 4 5 6 7

2. Estimate the extent to which social interactions **with other snow leopards** are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the snow leopard. Use as many social interactions that you can recall as a basis for your judgment.

least most
1 2 3 4 5 6 7

3. Estimate the extent to which social interactions **with keepers or other people** are satisfying, enjoyable experiences as opposed to being a source of fright, distress, frustration, or some other negative experience. It is not the number of social interactions that should be estimated, but the extent to which social interactions that do occur are a positive experience for the snow leopard. Use as many social interactions that you can recall as a basis for your judgment.

least						most
1	2	3	4	5	6	7

4. Estimate, for this snow leopard, the extent to which it is effective or successful in achieving its goals or wishes. Examples of goals would be achieving desired locations, devices, or materials in the enclosure. Keep in mind that each snow leopard will presumably have its own set of goals that may be different from other snow leopards.

least						most
1	2	3	4	5	6	7

5. Imagine how happy you would be if you were this snow leopard for a week. You would be exactly like this snow leopard. You would behave the same way as this snow leopard, would perceive the world the same way as this snow leopard, and would feel things the same way as this snow leopard.

least						most
1	2	3	4	5	6	7

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RESEARCH ARTICLE

Personality Assessment in Snow Leopards (*Uncia uncia*)

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Knowledge of individual personality is a useful tool in animal husbandry and can be used effectively to improve welfare. This study assessed personality in snow leopards (*Uncia uncia*) by examining their reactions to six novel objects and comparing them to personality assessments based on a survey completed by zookeepers. The objectives were to determine whether these methods could detect differences in personality, including age and sex differences, and to assess whether the two methods yielded comparable results. Both keeper assessments and novel object tests identified age, sex, and individual differences in snow leopards. Five dimensions of personality were found based on keepers' ratings: Active/Vigilant, Curious/Playful, Calm/Self-Assured, Timid/Anxious, and Friendly to Humans. The dimension Active/Vigilant was significantly positively correlated with the number of visits to the object, time spent locomoting, and time spent in exploratory behaviors. Curious/Playful was significantly positively correlated with the number of visits to the object, time spent locomoting, and time spent in exploratory behaviors. However, other dimensions (Calm/Self-Assured, Friendly to Humans, and Timid/Anxious) did not correlate with novel-object test variables and possible explanations for this are discussed. Thus, some of the traits and behaviors were correlated between assessment methods, showing the novel-object test to be useful in assessing an animal's personality should a keeper be unable to, or to support a keeper's assessment. Zoo Biol 31:151–165, 2012. © 2011 Wiley Periodicals, Inc.

Keywords: personality; individual differences; snow leopard; welfare

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INTRODUCTION

Although the scientific study of personality in animals is relatively new [Gosling and John, 1999], it has engendered a large body of literature, including studies of domestic cats [*Felis catus*, Feaver et al., 1986], cheetahs [*Acinonyx jubatus*, Wielebnowski, 1999], clouded leopards [*Neofelis nebulosa*, Wielebnowski et al., 2002], horses [Lloyd et al., 2007], giant pandas [*Ailuropoda melanoleuca*, Powell and Svoke, 2008; Powell et al., 2008], and many more [see Gosling, 2001, for a review]. Overwhelmingly, these studies have found that personality does exist within nonhuman species [Gosling, 2008]. Both age and sex differences have also been found in animal personality studies [e.g., Stevenson-Hinde et al., 1980a,b; Wielebnowski, 1999; King et al., 2008]. In addition, personality assessment is increasingly being studied as a tool to understanding an animal's welfare [e.g., Vazire et al., 2007; Weiss et al., 2002, 2006; King and Landau, 2003].

Assessment of animal personality by zookeepers has been shown to be consistent with direct behavioral observations [e.g., Pederson et al., 2005; Carlstead et al., 1999; Wielebnowski, 1999; Momozawa et al., 2003]. These studies give support to the practice of measuring personality by relating survey answers with behavioral assessments. In addition, a recent review of studies involving human assessments of animal personality [Meagher, 2009] concluded that trait ratings are not only accurate but also advantageous in both practical and scientific ways. For instance, they are noninvasive and they can be used to integrate multimodal information (behavior across situational contexts and time). Most important, the methods used in these studies—questionnaires and behavioral assessments—produce consistent results that, therefore, can be used to predict behavior.

If accurately assessed, personality can be useful for animal management. In any species, knowing the personality of each animal may facilitate breeding. Wielebnowski [1999] suggested that assessing behavior could allow predictions of reproductive success on an individual level. Cheetahs that scored high on the dimension tense–fearful were hypothesized to have more difficulty coping with the captive environment, and therefore need more seclusion and more places to hide in order to breed successfully. Powell et al. [2008] found that high scores on shyness in giant pandas were correlated with poorer sociosexual performance. Based on that finding, the authors suggested that altering enclosures (providing environmental enrichment and more dens), increasing comfort levels with keepers, and reducing stress could improve reproductive success because these manipulations might reduce shyness.

In order for keepers to form a valid judgment of personality, a certain amount of experience with an animal is necessary [Highfill et al., 2009]. That time may not be available, in some cases. It would be an advantage, therefore, to have another valid assessment method (in addition to keeper assessment) that is time efficient [Seaman et al., 2002]. Carlstead et al. [1999], Wielebnowski [1999], and Powell and Svoke [2008] demonstrated that the novel-object test could be a quick personality assessment tool.

Powell and Svoke [2008] paired keeper assessments with a novel-object test with giant pandas as a rapid means of assessing personality. They found that there was consistency between their assessment methods (keeper assessments and behavioral profiles of reaction to novel objects), and concluded that a novel-object test might also have predictive value for personality. However, owing to the small

sample size ($n = 4$), these findings require validation with a larger sample size and a different species.

In this study, we focused on comparing direct behavioral observations of captive snow leopards (*Uncia uncia*) to keepers' assessments of personality traits—that is, adjectives that could be combined to form a good descriptor of a personality type or dimension. We looked at age and sex differences in the collection of snow leopards. Based on previous studies, we expected that both the keeper assessments and the novel-object tests would reliably distinguish differences in personality among individuals and that the results of each type of test would be consistent with one another.

METHODS

Subjects and Housing

Snow leopards are a good choice for novel-object studies because they are solitary in the wild. Thus, their behavioral responses to novel objects should reflect real individual differences in personality that are independent of social influences. Eleven snow leopards, 10 captive born at the Wildlife Conservation Society's Bronx Zoo in New York City, New York, United States, and one wild born, participated in this study. The group consisted of seven females and four males from various genetic lineages, aged from 2 to 19 years, with a mean age of 8.45 years (Table 1). On average, females were 1.25 years older than males. Two of the participating females were the dams to four other participating snow leopards; two of the participating males sired three participating snow leopards (Table 1).

The snow leopards' outdoor holding cages each measured 4.57×5.18 m. Within these enclosures were 1.22×2.44 m dens. The ground surfaces of the enclosures were soil and screening, and the walls were welded box wire. Each enclosure had a raised platform and raised large tree trunks lying within to provide opportunity for climbing. Guillotine doors were used for animal entry and exit.

For the behavioral assessment, 9 of the original 11 snow leopards were used. Two females, Mina and Misty, were still housed together and could not be tested independently. In addition, one female was removed from the experiment after three novel-object tests, because she consistently exhibited excessive pacing and hiding

TABLE 1. Descriptive Information of the Snow Leopards Participating in the Study

Name	Sex	Age (yrs)	Dam	Sire
Bach	M	15	Other	Other
Boris	M	11	Ivy	Bach
Bhutan	M	6	Mei Mei	Bach
Ivy	F	19	Other	Other
Leo (wild born)	M	3	Other	Other
Mei Mei	F	11	Other	Other
Mina	F	2	Mei Mei	Other
Misty	F	2	Mei Mei	Other
Sally Ann	F	19	Other	Other
Shelby	F	3	Other	Boris
Tashi	F	14	Other	Other

[a]Other refers to animals not at the Bronx Zoo.

when the novel object was placed in her enclosure. All three animals were included in the keeper assessments, and the data from the novel-object tests that the third female did complete, were included in the analysis.

Procedure

A survey was developed for the snow leopard keepers ($n = 8$) to answer, based on those used in other studies of felids [Feaver et al., 1986, for domestic cats; Wielebnowski, 1999, for cheetahs; and Wielebnowski et al., 2002, for clouded leopards]. The survey asked the keepers to assess the personality of each of the animals in their care by presenting 21 definitions of personality traits (Table 2) and asking each keeper to rate each snow leopard on each trait on a nine-point Likert scale. A score of one represented "not at all" and a score of nine "very much so," making five the neutral score. Each keeper was given the questionnaire separately and instructed not to consult others in answering it so that their answers would represent only their own opinions based on their years of experience with the individual cats. They were instructed to consider the general impression of each trait and not to focus on a specific event.

After the completion of the surveys by the keepers, a novel-object test was given to each of the snow leopards. Six novel objects, including a plastic planter, a keg-shaped cooler, a round buoy, a trash can, a plastic gas can, and four-inch plastic drain piping, were each placed separately at different times in each animal's outdoor holding cage, where it would see the object immediately when the door to the cage opened. Every object was given to each animal in random order and animals were selected randomly for each test as well. The snow leopards could not see each other during

TABLE 2. Definitions of Adjectives Used in the Survey for Keeper Assessments

Active: Moves frequently (e.g., paces, runs, stalks often)
Aggressive to people: Reacts in a hostile way or attempts to attack/threaten people
Anxious: Interested but fearful and uneasy; vacillates between approach and withdrawal
Calm: Not easily disturbed by changes in the environment
Cooperative: Is compliant; willingly behaves when asked to do something
Curious: Seeks out or investigates novel situations
Depressed: Failure to seek out or respond to social interactions (inactive, unresponsive, asocial)
Eccentric: Shows stereotypic or unusual behaviors
Excitable: Overreacts to changes in the environment
Fearful of people: Retreats readily from people
Friendly to people: Initiates proximity; approaches fence readily and in a friendly manner (e.g., purrs, rubs on fence)
Insecure: Seems scared easily; "jumpy" and fearful in general
Playful: Initiates and engages in play behavior (seemingly meaningless, but nonaggressive behavior) with objects
Self-assured: Moves in a seemingly confident, well-coordinated, and relaxed manner
Smart: Learns quickly to associate certain events, appears to remember for a long time
Solitary: Spends time alone; avoids company
Tense: Shows restraint in movement and posture
Timid/shy: Reluctance to approach other animals, novel objects, or new situations
Trusting: Not suspicious; approaches easily
Vigilant: Watchful, observant; spends a lot of time attending to its surroundings
Vocal: Frequently and readily vocalizes

TABLE 3. Ethogram of Behaviors Scored During Novel-Object Tests

Contact	Touches object with any body part (duration)
Den	Most or all of the body is in the den, all four legs within the den
Exploratory	Flehmen (opens mouth and upper lip) or sniffing air, substrates, or object
Latency	Elapsed time between having access to the object and making first contact with the object
Locomotion	Walking, running, trotting, or other movement on all four limbs
Lying	Lying down, with all four limbs and belly on the ground
Marking	Marking, including treading, spraying, rubbing facial glands
Object visits	Visits (contact required) to the object (frequency) (separated by >5 sec)
Sitting	Sits on hind limbs
Stereotypic	Stereotypic behaviors, including pacing, self-biting, and fur plucking
Visits	Visits to the indoor quarters door (separated by >5 sec)
Other	Behaviors not covered in ethogram, including eating and drinking
Out of sight	Not visible on camera

these tests. The novel-object tests were carried out in the early afternoon from August to November 2007, and the behavior of each snow leopard with each object was filmed between 13:30 and 15:30 hr for 20 min each. Animals were shifted out of the enclosure first or locked in the dens for object placement. Sampling began when the snow leopard entered the enclosure. Reactions to the novel object were videotaped with a Sony Handcam (Sony Corporation of America, New York, NY) by the second author from outside the enclosure. Objects were cleaned between trials, to remove the effect of conspecific scent on the objects.

An ethogram for this experiment (Table 3) was developed by combining behavioral definitions from Wielebnowski et al. [2002], Powell and Svoke [2008], and Powell et al. [2008]. The ethogram measured latency to touch the object, total contact time with the object, number of visits to the object (separated by >5 sec), number of visits to the den door (separated by >5 sec), time spent in the den, time locomoting, time engaged in exploratory behavior (including flehmen—a behavior used to access a secondary olfactory system that detects chemical substances [Mellen, 1993]—and sniffing), number of scent marks, duration of stereotypic behaviors (including pacing, self-biting, and fur plucking), and proportion of time spent resting (lying or sitting down). Each behavior was chosen as possibly having a link to a personality trait; for instance, a bold animal may approach a novel object more quickly than a shy one. Strong correlations will suggest that both methods are assessing the same construct [Vazire et al., 2007].

Statistical Analyses

Data were analyzed using SPSS 15.0. Results were considered significant when $P<0.05$. In order to identify differences between females and males, independent sample t-tests were used, with Cohen's d to measure effect size. Pearson or Spearman correlations (depending on sample size and assumptions about distribution) were used to look for associations between age and keeper assessments and behavioral tests.

As in similar studies [e.g., Lloyd et al., 2007], Kendall's coefficient of concordance (W) was calculated to assess agreement among all raters on each personality trait for all animals. It was also calculated for all personality trait scores for each snow leopard across eight raters. A Spearman's rank-order coefficient (r_s) between the values on all traits for an animal as rated by pairs of keepers was calculated for each personality trait score across snow leopards to assess reliability of

the keepers' assessments. This was repeated for all animals and all possible pairings of keepers. All correlations for a personality trait had to be statistically significant for it to be considered reliably rated and included in the analyses. After the removal of unreliable personality traits, W was recalculated for all 11 snow leopards.

Finally, a matrix of Pearson correlation coefficients was calculated and used to reduce the 18 personality trait scores to five dimensions of significantly correlated behaviors [Carlstead, 1998]. A score was calculated for each snow leopard equaling the sum of the ratings of each keeper for each personality trait score in the five dimensions [Powell and Svoke, 2008]. Cronbach's α was used to measure the internal consistency of the five dimensions, with a result of 0.7 or above considered a high result [Bland and Altman, 1997].

These scores were then compared with the results from the novel-object tests (values for which were averaged across trials) using Spearman's rank-order coefficients (r_s). Pearson and Spearman correlations and t-tests were used to identify age and sex differences, respectively. Data for the snow leopard that was removed from the study were included in analysis, because they were consistent across the three trials in which she did participate.

RESULTS

Keeper Assessment

All the keepers' assessments of the snow leopards were significantly correlated across animals, showing agreement among raters on traits: Kendall's correlation coefficients (W) by animal varied from 0.211 to 0.660 (all tests: $df = 10$, $P < 0.05$, individual results not shown). Three of the personality trait scores were not reliably rated across snow leopards and raters: depressed ($W[10] = 0.283$, $P = 0.074$), smart ($W[10] = 0.211$, $P = 0.069$), and solitary ($W[10] = 0.225$, $P = 0.339$), and so were excluded from further analysis.

The keepers were found to be consistent in their assessments of personality, with some positive correlations found between all pairs of keepers for all behavioral adjectives. Significant Spearman's rho (r_s) values ranged from 0.603 to 0.962 (all tests: $df = 10$, $P < 0.05$, individual results not shown).

Reduction to Five Dimensions

The number of behavioral adjectives was reduced to five dimensions—Active/Vigilant, Timid/Anxious, Calm/Self-Assured, Curious/Playful, and Friendly to Humans (Table 4)—using a matrix of Pearson correlation coefficients (r), with values ranging from 0.639 to 0.945 (all tests: $df = 10$, $P < 0.05$, significant results in Table 5).

TABLE 4. Number of Behavioral Adjectives Was Reduced to Five Dimensions

Dimension	Active/ Vigilant	Timid/ Anxious	Calm/Self-Assured	Curious/ Playful	Friendly to Humans
Personality traits	Active, vigilant	Anxious, fearful, insecure, tense, timid, eccentric, excitable	Calm, self-assured	Curious, playful	Cooperative, friendly, trusting
Cronbach's α	0.712	0.962	0.849	0.851	0.911

TABLE 5. Significant r Values (All Tests: df = 10, $P < 0.01$) From the Matrix of Pearson Correlation Coefficients Used to Reduce the Number of Behavioral Adjectives to Five Dimensions

	Active										
Vigilant	0.702										
Calm		Calm									
Self -assured		0.752									
Curious			Curious								
Playful			0.761								
Anxious				Anxious							
Fearful				0.809	Fearful						
Insecure				0.875	0.827	Insecure					
Tense				0.873	0.905	0.893	Tense				
Timid				0.854	0.846	0.893	0.922	Timid			
Eccentric				0.722	0.736	0.750	0.860	0.860	Eccentric		
Excitable				0.807	0.694*	0.857	0.749	0.749	0.836		
Cooperative										Cooperative	
Friendly										0.774	Friendly
Trusting										0.879	0.945

*$P < 0.05$.

Male vs. Female Personality Traits

There were significant differences between males and females in some of the individual personality traits. Males were rated as more vigilant ($t[9] = 3.22$, $P = 0.011$, $d = 2.15$) and vocal ($t[9] = 3.59$, $P = 0.006$, $d = 2.39$). The difference in male vs. female behavior for curious approached significance, with males tending to be more curious ($t[9] = 2.07$, $P = 0.068$).

In terms of the larger personality dimensions, males were more Active/Vigilant than females ($t[10] = 2.37$, $P = 0.042$), but did not differ from females in any of the other trait dimensions (results not shown).

Age Differences

Keeper scores on some individual adjectives were significantly correlated with age across snow leopards, and within sex for females (Table 6, A and B). There were no significant correlations between keeper scores and male age, although calm ($r[3] = 0.924$, $P = 0.076$), playful ($r[3] = -0.950$, $P = 0.050$), and trusting ($r[3] = 0.924$, $P = 0.076$) approached significance. Some of the five dimensions significantly correlated with age as well (Table 6, C and D; Fig. 2).

Individual Differences

Within sex, there was notable variation across individuals (Fig. 1), and variance in Active/Vigilant was higher in females ($s^2 = 301.29$) than males ($s^2 = 113.67$). Three of the females had Active/Vigilant scores comparable to those of males, whereas the

TABLE 6. Keeper Scores and Age, Compared Using Pearson Correlations

Personality trait	Pearson correlation
A. Results from all snow leopards on personality traits	
Calm	$r[10] = 0.748$, $P = 0.008$
Active	$r[10] = -0.796$, $P = 0.003$
Excitable	$r[10] = -0.783$, $P = 0.004$
Fearful	$r[10] = -0.658$, $P = 0.028$
Insecure	$r[10] = -0.625$, $P = 0.040$
Playful	$r[10] = -0.895$, $P = 0.000$
B. Results from female snow leopards on personality traits	
Active	$r[6] = -0.923$, $P = 0.003$
Excitable	$r[6] = -0.774$, $P = 0.041$
Playful	$r[6] = -0.912$, $P = 0.004$
Personality dimension	**Pearson correlation**
C. Results from all snow leopards on personality dimensions	
Calm/Self-Assured	$r[10] = 0.617$, $P = 0.043$
Active/Vigilant	$r[10] = -0.682$, $P = 0.021$
Curious/Playful	$r[10] = -0.762$, $P = 0.006$
Timid/Anxious	$r[10] = -0.609$, $P = 0.047$
Personality dimension females	**Pearson correlation**
D. Results from female snow leopards on personality dimensions	
Active/Vigilant	$r[6] = -0.829$, $P = 0.021$
Curious/Playful	$r[6] = -0.797$, $P = 0.032$

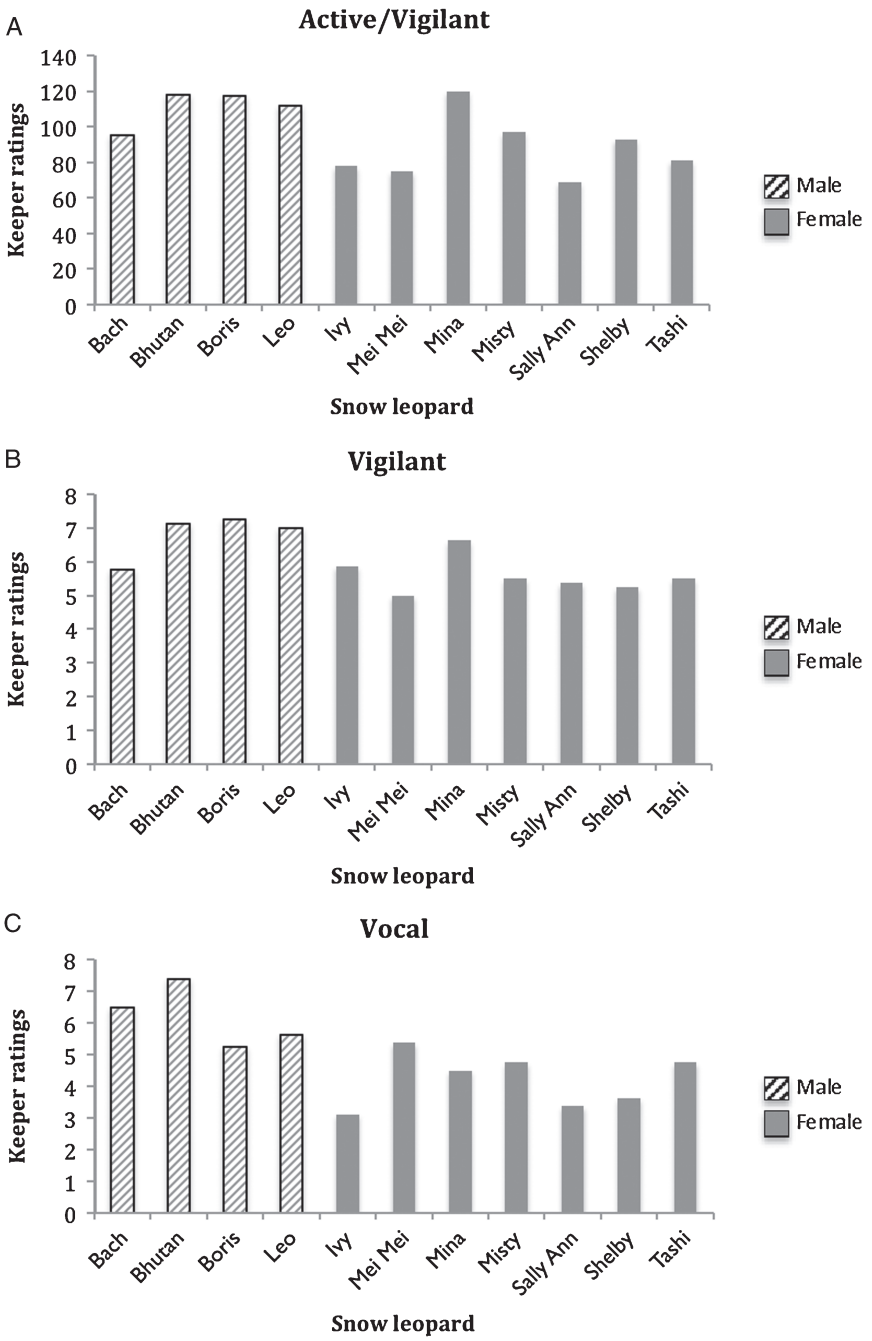

Fig. 1. Although male snow leopards were generally rated as more Active/Vigilant (**A**), vigilant (**B**), and vocal (**C**) than females, variation exists among individuals.

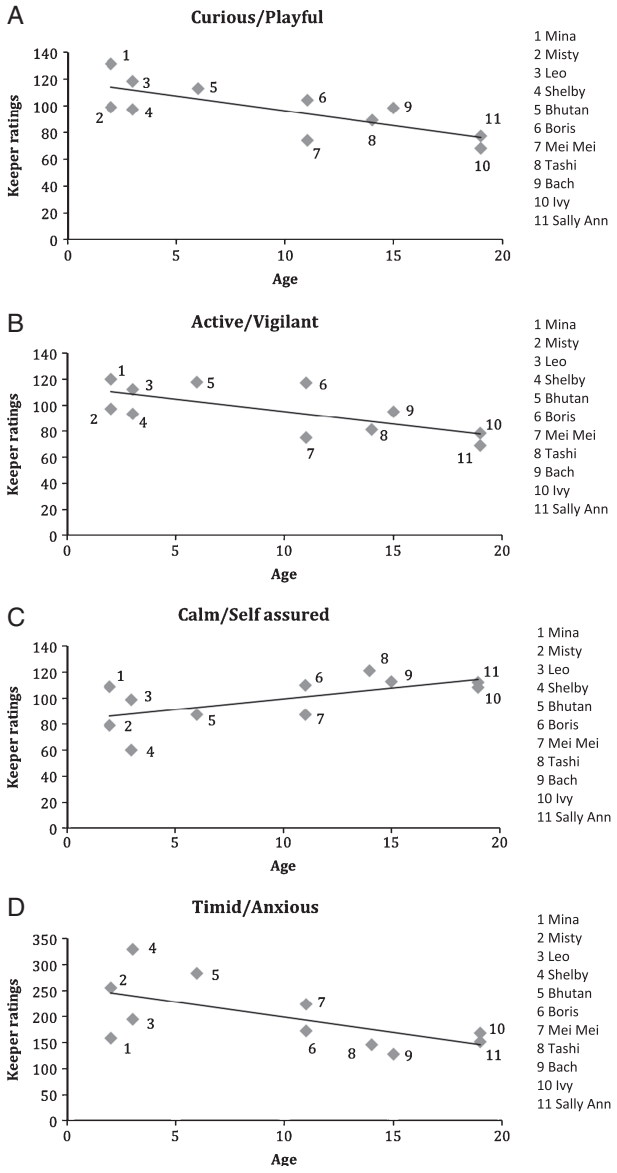

Fig. 2. Age effects play a role in personality, but individual variation is still apparent. Particularly notable are the differences between Mina and Misty, both age 2; Leo and Shelby, age 3; Boris and Mei Mei, age 11; and Bach (age 15) and Tashi (age 14). (Regression lines shown for illustration purposes only.) (**A**) As snow leopards age, they are rated as less Curious/Playful. (**B**) As snow leopards age, they are rated as less Active/Vigilant. (**C**) As snow leopards age, they are rated as more Calm/Self-Assured. (**D**) As snow leopards age, they are rated as less Timid/Anxious.

other females' scores were lower. Variance in vigilant was higher in males ($s^2 = 0.48$) than females ($s^2 = 0.28$), and two of the females had vigilant scores comparable to those of the males, whereas the other females' scores were lower. Variance was also

higher in males in vocal (males $s^2 = 0.90$; females $s^2 = 0.71$) and only one female's score on vocal was comparable to that of the males, with the rest lower.

Age differences were also variable across individuals (Fig. 2), and variance in Curious/Playful was highest in mid-aged animals (6–11 year olds) ($s^2 = 417$) and lowest in older animals (14–19 year olds) ($s^2 = 174$); young animals (2–3 year olds) were in the middle ($s^2 = 262.917$). Variance in Active/Vigilant was also highest in mid-aged animals ($s^2 = 602.333$) and lowest in older animals ($s^2 = 116.250$); young animals were in the middle ($s^2 = 160.333$). Variance in Calm/Self-Assured was highest in the youngest animals ($s^2 = 473.583$) and lowest in older animals ($s^2 = 29.667$); mid-aged animals were in the middle ($s^2 = 176.333$). Similarly, variance in Timid/Anxious was highest in the youngest animals ($s^2 = 5{,}628.250$), lowest in older animals ($s^2 = 286.250$), with mid-aged animals in the middle ($s^2 = 3{,}084.333$).

Novel-Object Tests

Males spent significantly more time in exploratory behaviors ($t[8] = 3.51$, $P = 0.010$), scent marked ($t[8] = 2.46$, $P = 0.043$), and visited the object ($t[8] = 2.76$, $P = 0.028$) significantly more times than females. There were no significant correlations between novel-object test behaviors and age overall. Within sex, older females spent more time in contact with objects ($r[4] = 0.889$, $P = 0.044$). There were no significant correlations between novel-object test behaviors and male age.

Comparing Keeper Assessments and Behavioral Tests

The dimension Active/Vigilant was significantly positively correlated with number of visits to the object ($r_s[8] = 0.740$, $P = 0.023$), time spent locomoting ($r_s[8] = 0.750$, $P = 0.020$), and time spent in exploratory behaviors ($r_s[8] = 0.750$, $P = 0.020$). Curious/Playful was significantly positively correlated with number of visits to the object ($r_s[8] = 0.790$, $P = 0.011$), time spent locomoting ($r_s[8] = 0.767$, $P = 0.016$), and time spent in exploratory behaviors ($r_s[8] = 0.733$, $P = 0.025$). The dimensions Calm/Self-Assured, Friendly to Humans, and Timid/Anxious did not correlate significantly with any of the novel-object test variables.

DISCUSSION

Gosling and John [1999] reviewed 19 studies of personality across 12 nonhuman species using the Five-Factor Model [John, 1990; Costa and McCrae, 1992], a hierarchical model of personality that was initially used with humans. The authors found that three of these factors: extraversion vs. introversion, neuroticism vs. emotional stability, and agreeableness vs. antagonism generalized the most across species. Openness vs. closed to experience followed, with seven of the species studied showing such traits. Finally, the factor labeled conscientiousness was only found in chimpanzees and humans.

In this study, the reduction of traits to five dimensions was consistent with this model. Four of five dimensions found in this study can be compared with the Five-Factor Model. Active/Vigilant matches best with extraversion vs. introversion, Timid/Anxious and Calm/Self-Assured with neuroticism vs. emotional stability, Calm/Self-Assured and Friendly to Humans with agreeableness vs. antagonism, and

Curious/Playful with open vs. closed to experience [note that cats were one of the seven species showing this dimension in the Gosling and John, 1999, review].

Questionnaire

Keepers' assessments of personality were reliable; that is, they were consistent across keepers, as they have been in other felid studies [Feaver et al., 1986; Wielebnowski, 1999; Wielebnowski et al., 2002]. Interrater agreement was high. On average, keepers had spent 3 hr per week with the snow leopards over a period of 3 years. Because the keepers were instructed not to discuss their answers to the survey, as in other studies [Lloyd et al., 2007], they were considered independent. However, because their assessments of personality were based on a composite view over time, it is possible that discussions had occurred in the past about the animals' personality. It is highly unlikely, however, that such discussions used the precisely defined adjectives and their definitions provided in the survey (aggregates of which became the overall personality type). In addition, because of the extensive use of trait rating in the literature, with significant results across species and with the accompanying statistical tests, shared stereotypes are unlikely [McCrae, 1982]. Finally, the ratings can be considered unbiased, because they were subjected to statistical tests that affirm both reliability and validity [Meagher, 2009].

There were few differences in how keepers rated males vs. females. This was an expected result, as female and male behavior in the wild tends to be similar [Freeman, 1983]. Differences existed in levels of activity, vigilance, and vocalization, which were higher in males. In the wild, male snow leopards have a larger home range than females [Jackson, 1996]. They have to compete with other males to breed and sometimes for territory, and to look for females with whom to breed. Vocalizations in snow leopards seem to be used especially for breeding purposes [Nowak, 1999; Jackson, 1996]. Although males showed higher levels of these activities, there was variation among the individuals (see Fig. 1). Therefore, we can assume that while there are some sex effects, individual differences still exist.

Age has been shown to correlate with personality [e.g., see Weiss et al., 2007]. Because younger mammals often play more than older ones [Bekoff and Byers, 1998], testing motor skills and learning behaviors, such as fighting, copulatory positions, and social hierarchies, it makes sense that the younger the snow leopards are the more they were rated as Curious/Playful and the older the less they were rated Active/Vigilant (a result also seen in females alone). Older snow leopards were rated as more Calm/Self-Assured and less Timid/Anxious, an expected result of aging; though these general trends show age effects in personality, variation is still seen in the individual results (see Fig. 2). Notably, there were marked differences between snow leopards at the same age; for instance, between Mina and Misty (age 2), Leo and Shelby (age 3), Boris and Mei Mei (age 11), Bach (age 15) and Tashi (age 14), and Ivy and Sally Ann (age 19). Variation was also seen within age groups, at its highest in mid-aged animals for Curious/Playful and Active/Vigilant and in the youngest animals for Calm/Self-Assured and Timid/Anxious.

The results suggest that personality may continue to be refined or shaped by experience into adulthood. The lack of significance with other dimensions may suggest that certain dimensions of personality are under more genetic control or may be the result of the small sample size, an issue that should be kept in mind in considering results throughout this research. Further research would be helpful.

Novel-Object Tests

In the novel-object tests, males visited the object and scent marked significantly more than females and showed significantly more exploratory behaviors. This fits well with snow leopard biology. As mentioned earlier, larger home ranges in the wild may explain why males show more activity in captivity than females do; in addition, they also compete with other males for territory and for breeding. Both these behaviors may lead to increased scent marking and exploratory behaviors in captivity.

There were no significant correlations with age for the novel-object tests for all the snow leopards, but older females spent more time in contact with the object. As older females were less Curious/Playful, this is an interesting result. It may be explained by the older snow leopards being more Calm/Self-Assured as well. It is possible that being curious or playful did not define how they were interacting with the object. The nature of the time spent with the object (e.g., active manipulation of the object or simply resting on it) is likely important and would be helpful in clarifying some of the relationships among variables.

Because all participating animals had reached the average age of sexual maturity, it is possible that the lack of significant differences between age and any of the other novel-object test variables is to be expected, whereas keeper surveys reflect impressions gathered over many years of the animals' lives, including when some of them were young.

Questionnaire and Novel-Object Tests Compared

The personality dimensions correlated with the number of times visiting the object (Active/Vigilant and Curious/Playful), time spent locomoting (Active/Vigilant and Curious/Playful), and time spent in exploratory behaviors (Active/Vigilant and Curious/Playful). This suggests that these behaviors are good indicators of personality and that the two methods—trait ratings and novel-object tests—assess the same constructs. Likewise, Lloyd et al. [2007] suggested that personality might predict behavior in horses, owing to the strong links between the trait ratings and the observed behavior that they found. Wielebnowski [1999] also found significant correlations among 11 of the survey items she used to rate cheetahs and five of their behavioral responses. However, it is also possible that active may be too general a trait to include in future surveys. Activity could be manifested for a variety of reasons, for instance, curiosity or vigilance, and may indicate more than one personality type.

Interestingly, Calm/Self-Assured, Friendly to Humans, and Timid/Anxious did not correlate significantly with any of the novel-object test variables. When we went back to the individual survey items that made up each dimension, we did find that the item self-assured significantly (positively) correlated with the novel-object test behavior scent marking. Self-assured animals might be more likely to mark more often because they are more willing to announce their presence, and therefore open themselves to possible interactions with other snow leopards, including territorial fights for space or mates. Calm was defined as "not easily disturbed by changes in the environment" in the survey. The novel object should have qualified as a change in the environment, and because calm and self-assured were positively correlated, this result was unexpected. One explanation for this may be the novel objects themselves.

The majority of regular enrichment items for the snow leopards are large plastic items with similar characteristics to the novel objects used. Thus, the novel objects may not have been salient enough to qualify as a significant testing stimulus. Also, as a majority of the leopards in the novel-object test were older than age 10, it is possible that they were not as affected by changes in the environment as younger animals may have been. It could also be that the novel objects used here were not the most appropriate stimuli for these dimensions; for instance, a mirror might yield more salient results [as in Wielebnowski, 1999] or a stimulus affecting another sensory modality. Finally, although such tests have worked in other species, it is possible that the novel-object test did not completely reflect the dimensions of personality measured. Future studies should ensure that testing stimuli are truly novel and bear little similarity to stimuli the animals have experienced before.

The lack of significant correlation between questionnaire and novel-object tests in the dimension Friendly to Humans is understandable. In the novel-object tests, there was little human interaction and each of the adjectives included in this dimension depended on such interaction. These individual adjectives did not correlate significantly with the novel-object tests either. Half of the adjectives that comprised the dimension Timid/Anxious individually correlated significantly with the novel-object test variables (anxious, fearful, and timid) and half did not (eccentric, insecure, and tense). This contributed to the dimension not correlating significantly with the novel-object tests on the whole. Interestingly, when the first three were grouped as a dimension, there were still no significant correlations with the novel-object test variables. It is possible that the test stimulus was not novel enough to elicit fear or anxiety.

CONCLUSIONS

1. Keeper assessments of snow leopard personality are reliable for most traits.
2. There are sex effects on personality in this group of captive snow leopards.
3. Certain behaviors recorded during the novel-object tests had predictive value for personality and were consistent with keeper assessments.
4. The novel-object test can be helpful in assessing personality in animals quickly, and therefore can provide valuable information on how to care for individuals in captivity.

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Review

Personality in felids: A review

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ABSTRACT

Although there has been an increase in felid personality research, much more work is needed, with only 20 published studies, 17 of which focused on the domestic cat. Most studies show important implications for this type of research, but there is no consensus on terminology, method, or conclusions for felids, even at the species level. Felid personality research comes from various fields, and is often carried out with different methods, with diverse goals. This review evaluates the published research on felid personality, and addresses its reliability and validity. Only 60% of the studies reported reliability estimates, and these varied greatly across personality dimensions. The sample weighted mean correlation of the reliability estimates was 0.68 (based on three studies). Fifty-five percent of the studies assessed validity. The personality dimensions with the highest validity for all species were Sociable, Dominant, and Curious, with a mean correlation of 0.82. Recommendations for future research and implications for aiding in conservation and captive animal management efforts and improving health and well-being and welfare are discussed.

Contents

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1. Introduction

In the past decade, the study of nonhuman animal personality has greatly increased, leading to a literature that crosses both species (e.g., fish, birds, primates, dogs, felids) and fields (e.g., psychology, biology, genetics, veterinary studies) (Gosling, 2001). As in humans, personality in animals can have implications for behavior (Powell and Gartner, 2011), coping with stress (Wielebnowski et al., 2002), and well-being (King and Landau, 2003; Weiss et al., 2006, 2011). It also plays a role in conservation, including reintroduction efforts (e.g., Bremner-Harrison et al., 2004) and breeding success (Carlstead et al., 1999; Powell and Svoke, 2008). As a result, the study of personality has been used to address challenges for captive populations in laboratories, research centers, shelters, and zoos; as well as adding to our understanding of free ranging and homebound domestic animals (e.g., Feaver et al., 1986; Jones and Gosling, 2005).

Regardless of the increase in personality literature, there is a bias toward studying species that are more closely related to, or more closely associated with, humans. Among mammals, this has led to a good amount of literature on personality in nonhuman primates (210 articles, Freeman and Gosling, 2010), for example. There is also a growing literature on dog personality (51 articles, Jones and Gosling, 2005 or 56 with the inclusion of other canids, Gosling, 2001). By comparison, there are only 20 articles on personality in cat species.

By far, the most studied cat species, in terms of personality, is the domestic cat (*Felis silvestris catus*) ($n = 17$). Other species studied include snow leopards (*Uncia uncia*; Gartner and Powell, 2012), cheetahs (*Acinonyx jubatus*; Wielebnowski, 1999), clouded leopards (*Neofelis nebulosa*; Wielebnowski et al., 2002), and tigers (*Panthera tigris tigris*; Phillips and Peck, 2007); however, there has only been one published article on each of these species.

The implications of felid personality research are far reaching. Approximately 59% of cat species are endangered or in decline, their survival may thus depend on their success in zoos. However, because cat species naturally have large ranges, they often face challenges in zoo enclosures (Clubb and Mason, 2003). In small cages in shelters and laboratories felid welfare is often compromised as well. While various techniques have been utilized in increasing welfare, some species still face challenges in captivity. It is possible that assessing elements of individual differences can help to address some of these issues. For example, Wielebnowski (1999) suggests that cheetahs high on the dimension Tense-Fearful might have more difficulty in coping with the captive environment, and might therefore need more secluded enclosures and/or more hiding places.

In addition to using personality to address issues of welfare, it also is associated with overall well-being and physical health (Deary et al., 2010), and can play a role in conservation efforts (Carlstead et al., 1999; Powell et al., 2008) and captive animal management (Watters and Powell, 2012). In terms of both welfare and conservation, then, personality has the potential to play an important role that is, at the moment, underutilized.

The objective of this study is to provide an overview of the current work on felid personality, analyzing both the reliability and the validity of data available, and the implications for this type of research. Similar reviews have been carried out with primates (Freeman and Gosling, 2010) and dogs (Jones and Gosling, 2005)—the methods utilized here followed the latter in part.

2. Terminology

Although much discussed, terminology still presents somewhat of a problem in animal personality research, with the terms personality, temperament, coping styles, and behavioral syndrome all being used. Gosling (2008) states that the terms can be used somewhat interchangeably, although he argues for the use of the term personality to become more widespread for various reasons (Weinstein et al., 2008), the most important being assurance that the same thing is being discussed across fields. Across the research in this paper, the terms individual differences, temperament, personality, and behavioral styles are used, all generally to mean behaviors that are relatively consistent across both time and context. All the studies included were judged to be measuring some aspect of personality, as they included numerous hours of observation (two hours has been shown to be sufficient to make reliable judgements [Vazire et al., 2007], but all the studies had many more than that) and various contexts for their measurements. Because numerous methods are used to conduct the research, it is possible that one study's trait labeled "sociable" may not be the same as another study's trait labeled "sociable" (Carter et al., 2012). Therefore, studies were grouped together based not on choice of labels (for instance both "pace" and "external awareness" were placed in the general group "Active," along with traits labeled simply "active"), but on either testing or descriptive characteristics that made them similar.

3. Methods

3.1. Literature search

Using keywords for cat species including both common and scientific names, and the terms personality and temperament, a literature search was carried out in PsychInfo, CAB Abstracts, and ISI Web of Knowledge (which includes Web of Science, BIOSIS, and Medline). All articles included were from peer-reviewed journals and had to focus on personality directly. In other words, articles that mentioned some sort of personality construct, but did not actually assess personality in cats were not included. For example, Podberscek et al. (1991) conducted a behavioral assessment of laboratory cats in a familiar/unfamiliar person test. However, they were interested in the frequency of behaviors and therefore did not directly address personality constructs, although they included individual variation and dominant behavior. Similarly, Mertens and Turner (1988) discuss domestic cat individuality in terms of interactions with humans; in fact individuality was the most important factor of those measured influencing their behavior. However, the terms "shy" and "trusting" are not introduced until Section 5, and there is no explicit definition of those terms—the authors state that it was not their goal to define behavioral profiles.

3.2. Statistical analyses

Following Jones and Gosling's (2005) review of dog research, both reliability and validity of the current research in cat personality was assessed. Reliability, when results occur dependably, is a fundamental measure of consistency (Gosling, 2001). Along with validity, which measures how well an assessment tool is assessing what it is meant to determine, reliability reflects the value of the assessment tool being used.

Reliability can be measured in a number of ways, including measuring inter-rater reliability, internal consistency, or test-retest reliability (Jones and Gosling, 2005). Most of the studies in this review measured inter-rater reliability, except where noted. Therefore, minimum and maximum correlations for inter-observer agreement were reported for each study where possible (and percentages for three of the studies). Mean correlations were calculated for each measure used in a study, and the unweighted and sample-weighted means were calculated across studies. Spearman correlations between measures (for example survey and behavioral observations) were reported for each study that assessed convergent validity, which demonstrates strong correlations among measures assessing one construct. Unweighted and sample-weighted means were calculated and confidence intervals were calculated based on unweighted means (Jones and Gosling, 2005) for each dimension for all species, for domestic cats, and for wild species.

4. Results

There are many different personality traits measured in cats, with a few similarities across all species, including those related to activity or extraversion (active, curious, bold, excitable, extraversion, dominance); sociability (friendly, agreeable, social, extraversion); neuroticism (tense, hide, anxious, timid, fearful, staying indoors), and aggression (rough, aggressive). However, there is enough variability in terms, and some terms that were only found once (arrogant/calculating, conscientiousness, intellect/openness, trusting, and calm/self assured), that there is a need to standardize and validate the terms found, so that a meaningful discussion can be had.

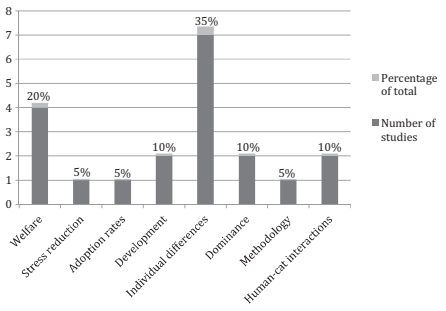

Fig. 1. Research goals of the cat personality studies reviewed, in percentage of the total and total number out of 20.

4.1. Types of research

4.1.1. Personality assessment

While assessment methods were varied, there were some consistencies in personality and behavioral methods (Table 1). Among animals in zoo environments, surveys were always used. Half of those studies also used behavioral tests, one novel object (Gartner and Powell, 2012) and one mirror stimulation (Wielebnowski, 1999) test. Research facilities generally carried out some sort of behavioral assessment (for example, observations, novel object tests, and unfamiliar person tests), with only two using a survey (Feaver et al., 1986; Turner et al., 1986). Finally, research conducted in private homes generally used behavioral observations or surveys, with two carrying out novel object tests (Durr and Smith, 1997; Meier and Turner, 1985).

4.1.2. Research goals

The studies varied in their goals as well (Fig. 1). Most of the zoo studies had a similar goal—to increase the welfare of the animal. On the other hand, research facilities mainly addressed how to reduce stress that leads to aggression toward handlers, although one (Siegford et al., 2003) addressed understanding personality as a goal to increasing adoption rates, and two looked at paternity and development (McCune, 1995 [and socialization]; Turner et al., 1986). The largest group, studies based on free-ranging cats or those already placed in homes, had varying goals including understanding individual differences and their implications (Bradshaw and Cook, 1996; Feaver et al., 1986; Lee et al., 2007; Lowe and Bradshaw, 2001; Meier and

Table 1
Summary of published felid personality research.

Author	Species	Sample size	Sex	Age	Environment	Methodology
Bradshaw and Cook (1996)	Domestic cat	36	17M/19F	6 months–over 8	Privately owned	Behavioral observations/survey
Durr and Smith (1997)	Domestic cat	22	9M/13F	5–11 years	Privately owned	Novel object/unfamiliar animal/object dominance
Feaver et al. (1986)	Domestic cat	14	Female	2.5–6.5	Research facility	Survey/Behavioral observations
Gartner and Powell (2012)	Snow leopard	11	4M/7F	2–19 years	Zoo	Survey/novel object
Gosling and Bonnenburg (1998)	Domestic cat	440	NR	NR	Privately owned	Survey
Iki et al. (2011)	Domestic cat	8	Male	2.75 years (onset)	Research facility	Tester interaction, ACTH, behavioral, surgery
Lee et al. (2007)	Domestic cat	196	NR	NR	Privately owned	Survey
Lowe and Bradshaw (2001)	Domestic cat	29	16M/13F	Birth–2 years	Privately owned	Behavioral observations
McCune (1995)	Domestic cat	37	19M/18F	Birth–1 years	Research facility	Novel object/unfamiliar person
Meier and Turner (1985)	Domestic cat	62	NR	NR	Privately owned	Novel object/unfamiliar person
Natoli et al. (2005)	Domestic cat	45	Male	NR	Free-ranging colonies	Behavioral observations
Phillips and Peck (2007)	Bengal tiger	7	6M/1F	2–9 years	Zoo	Survey
	Domestic cat	32	NR	5–20 weeks	Research facility	Handling during socialization/ACTH
Siegford et al. (2003)	Domestic cat	20	Female	10–18 months	Research facility	Novel object/unfamiliar person
Turner et al. (1986)	Domestic cat	40	NR	NR	Research facility	Survey
van den Bos and de Cock Buning (1994)	Domestic cat	10	Female	2–4 years	Research facility	Behavioral observations
van den Bos and de Vries (1996)	Domestic cat	25	Female	1–5 years	Research facility	Behavioral observations
Wedl et al. (2011)	Domestic cat	40	25M/15F	9 months–13 years	Privately owned	Survey/behavioral observations
Wielebnowski (1999)	Cheetah	44	19M/25F	3–13 years	Zoo	Survey/mirror test
Wielebnowski et al. (2002)	Clouded leopard	72	36M/36F	3–18 years	Zoo	Survey
Zeigler-Hill and Highfill (2010)	Domestic cat	106	NR	NR	Privately owned	Survey

NR: not reported.

Table 2
Inter-observer agreement (reliability) measures in felid personality assessment (Spearman's rho, except where noted).

Study	Inter-observer agreement					Number of items/*n*
	Mean/SE	Maximum		Minimum		
		Correlation	Item label	Correlation	Item label	
Durr and Smith (1997)	0.56/0.23	0.84[a]	Novel stimulus (group)	0.28[a]	Novel stimulus (individual)	7/22
Feaver et al. (1986)	0.63/0.30	0.91	Sociable with people	0.31	Solitary	18/14
Gartner and Powell (2012)	n/a	0.96[a]	Not specified	0.60[a]	Not specified	21/11
Turner et al. (1986)	n/a	0.96/0.90	Friendliness to humans (mothers/juveniles)			1/16
Turner et al. (1986)	n/a	0.74/0.43/0.48/0.47	Friendliness to humans (juveniles)			1/25
Turner et al. (1986)	n/a	0.72	Friendliness to humans (mothers)			1/22
Wielebnowski (1999)	0.75/0.16	0.98[a]	Eccentric	0.57[a]	Eccentric	18/44
Wielebnowski et al. (2002)	n/a/0.12	0.92[a]	Not specified	0.37[a]	Not specified	13/72
Unweighted mean	0.65					
Sample-weighted mean	0.68					

Note: only studies that specified all item correlations were included in the mean correlation (including unweighted and sample-weighted means).
n = sample size.
[a] Kendall correlation coefficients.

Turner, 1985; Natoli et al., 2005; van den Bos and de Vries, 1996), social dominance (Durr and Smith, 1997; van den Bos and de Cock Buning, 1994), assessing and solving problems of methodology (Gosling and Bonnenburg, 1998), and understanding human-cat interactions (Wedl et al., 2011; Zeigler-Hill and Highfill, 2010).

4.1.3. Age

Zoo studies had a large range of ages as zoos keep animals until they die ($n = 131$, $M = 7.95$ years, $SD = 2.25$). Domestic cat studies either did not report age ($n = 5$), or, excepting one, looked at young animals, up to 4 years ($n = 62$, $M = 4.83$ years, $SD = 2.09$). Bradshaw and Cook (1996) recorded age ranges (6 months to over 8 years) as owners were not always sure about exact ages. Lowe and Bradshaw (2001) tested animals at age 4, 12, and 24 months ($n = 29$). Feaver et al. (1986) tested two groups of seven cats (Group 1: $M = 5.1$, range = 2.5–6; Group 2: $M = 4.7$, range = 3–6.5). van den Bos and de Vries (1996) tested 29 cats, with ages ranging from 0.3 to 5 years. Research facilities all used young animals, under 3 years old ($n = 121$, $M = 1.55$ years, $SD = 1.60$).

4.1.4. Environment

There were four types of environment in the studies—research facilities (40% of studies), home environments (40% of studies), free ranging (5% of studies), and zoos (20% of studies). It is unknown whether environment plays a role in the behavior or personality of cats, but it is one possible explanation for the variance in results in the domestic cat, as personality may not be completely comprised of genetic makeup (Bell and Sih, 2007; Sih et al., 2004).

4.1.5. Breed and subspecies

Domestic cat breed was either not identified ($n = 11$) or domestic short hair cats were studied (Iki et al., 2011; McCune, 1995; Siegford et al., 2003; van den Bos and de Cock Buning, 1994; van den Bos and de Vries, 1996; Wedl et al., 2011 [plus two domestic long hairs]). The subspecies of tiger studied was the Bengal tiger (Phillips and Peck, 2007); the other zoo animals do not have subspecies.

4.1.6. Sexual status of subjects

Zoo animals were all intact, since breeding is a primary reason to keep endangered animals. Some of the domestic cats were intact, while some were neutered/spayed. Some studies specified how many of each; some did not. Personality after the fact may be an important construct, especially in shelter situations, where animals are almost always neutered/spayed, and where personality may play a role in adoption rates (Siegford et al., 2003).

4.2. Are the measures reliable?

Only 60% of the studies reported reliability of any kind. Six of these reported inter-observer agreement (Table 2). Six studies were not included in Table 2 because of the different methods they used to assess reliability. Two studies used Cronbach's alpha as a measure of internal consistency of each dimension measured across subjects (Gartner & Powell, 2012: mean $\alpha = 0.85$ [but also reported correlations and was therefore included in Table 2]; Zeigler-Hill and Highfill, 2010, mean $\alpha = 0.85$[1]). One used percentages of positive and negative results for the Feline Temperament Protocol (FTP; 88 and 92%, respectively) and percentages of intra- and inter-rater agreement for behavioral observations of two cats during a stress test (91 and 89%, respectively; Iki et al., 2011).

Meier and Turner (1985) showed test-retest reliability using frequencies, but did not report numerical values. Thirty-three of the cats in the study were encountered at least three times each in the behavioral analysis. Of these, 25 always had the same reaction: nine could always be

[1] This study reported an internal consistency coefficient, without specifying what type.

stroked, 16 always ran away. Based on these behaviors, the authors assessed two types of personality: shy and trusting.

Siegford et al. (2003) reported test-retest reliability for the FTP. The FTP measures general levels of sociability ("acceptable scores") and aggressiveness and adaptability to new situations ("questionable scores") (Lee et al., 1983). There was no statistically significant change over time for acceptable scores ($F[3,76] = 1.29$, $P = 0.28$), while questionable scores changed significantly over time ($F[3,76] = 6.01$, $P = 0.001$): 6 months after adoption, cats had lower questionable scores than second pre-adoption and 3 months post-adoption tests. However, while the authors reported high inter-observer reliability, they gave no numerical value. They did, however, report that mean acceptable scores on all FTPs were negatively correlated with mean questionable scores ($r = 0.85$, $P < 0.001$).

Wedl et al. (2011) reported the inter-observer agreement as 0.80, but gave no further details. Another study (Phillips and Peck, 2007) reported using Friedman's test (Friedman, 1937)—a non-parametric measure similar to repeated measures ANOVA.

Minimum correlations across the remaining studies ranged from 0.28 to 0.60 and maximum correlations ranged from 0.84 to 0.98. The sample weighted mean was 0.68, but this could only be calculated on three studies, due to the lack of available data. Mean inter-rater reliabilities varied from 0.56 to 0.75 for these three studies. It is clear that there is reliable inter-rater agreement on many of the items researched; however, enough studies did not include the statistics, and enough had low correlations so that overall reliability cannot be verified across these cat personality studies.

4.3. Are the findings valid?

Fifty-five percent of the studies measured validity. The convergent validities for Sociable, Dominant, Curious, and Active were strong. The convergent validities for Aggressive, Calm, Timid/Fearful, and Excitable were less so (Tables 3 and 4).

Six personality dimensions were measured by more than one study: Active, Aggressive, Curious, Dominant, Sociable, and Timid/Fearful. The mean validity coefficient for these dimensions was 0.68. Dimensions found in single studies included Calm, Excitable, and Self Assured (Wielebnowski, 1999), Shy (Meier and Turner, 1985), Subordinate (van den Bos and de Cock Buning, 1994), and Vocal and Voracious (Feaver et al., 1986). The validity measures are included in Table 4 for these studies, but means and confidence intervals were only calculated for Calm and Excitable, because multiple measures were used.

Siegford et al. (2003) reported validity data, but because they were using the FTP as a measure, the results were not included in this analysis. This is because the FTP only measures general levels of sociability and aggressiveness and adaptability to new situations. However, the results are still pertinent. They found that acceptable (sociability) scores on pre-adoption FTPs positively correlated with positive responses to familiar caretakers in rooms in which the cats were usually housed ($r = 0.51$, $P = 0.02$) and average percent of time spent near unfamiliar people in open field tests in novel rooms (men: $r = 0.60$, $P = 0.01$; women: $r = 0.57$, $P = 0.01$). They also found a positive correlation between questionable (aggressiveness/adaptability) scores on pre-adoption FTPs and percent of time cats spent in corners of the novel room during open field tests ($r = 0.51$, $P = 0.03$). Finally, the number of cell crossings in open field tests positively correlated with acceptable scores on pre-adoption FTPs ($r = 0.54$, $P = 0.02$).

Table 3
Convergent validities for the strongest and middle felid personality dimensions.

Dimension	UM	95% CI	SWM
Sociable	0.94	0.88, 0.94	0.93
Dominant	0.76	0.68, 0.81	0.74
Curious	0.75	0.65, 0.83	0.70
Active	0.72	0.49, 0.79	0.49
Aggressive	0.57	0.28, 0.78	0.48
Calm	0.40	0.16, 0.64	0.40
Timid	0.36	0.22, 0.49	0.34
Excitable	0.34	0.21, 0.47	0.34

UM = unweighted mean; SWM = sample-weighted mean; 95% CI = 95% confidence interval.

Iki et al. (2011) also used the FTP as a measure of personality, but found no behavioral correlates with it. However, acceptable scores correlated significantly with cortisol concentration during a spray bath stress test ($r_s = 0.70$, $P = 0.047$).

To assess whether the four studies on wild cats affected the results, validity was calculated for domestic cats and wild cats separately. For the wild cats, Active/Vigilant, Curious, and Timid/Fearful were assessed by more than one study. The convergent validities of these three personality dimensions were similar to the overall numbers reported above: Active/Vigilant (unweighted mean (UM) = 0.60, sample weighted mean (SWM) = 0.45, CI at 95% = 0.40–0.71) and Curious (UM = 0.73, SWM = 0.68, CI at 95% = 0.61–0.85). Timid/Fearful was not measured in domestic cats so the numbers did not change.

For the domestic cats, Curious/Playful, Dominant, and Sociable were measured by more than one study. Only Curious/Playful was measured in both species; for domestic cats alone, the means were similar to the overall and the wild cat results (UM = 0.77, SWM = 0.73), but the confidence interval was quite large (at 95% = 0.40–1.10). Only two studies looked at this dimension in domestic cats alone, though the environments were different, with one taking place in a research facility (Feaver et al., 1986) and one in the home (Durr and Smith, 1997). This may have influenced the results. In addition, Feaver et al. (1986) were measuring "Playful" while Durr and Smith (1997) were measuring "Attention Span"—it is possible that these two things were not similar enough to include in the same category.

5. Discussion

Of the studies reported here, 60% included information on reliability. Reliability varied greatly across personality dimensions and both within and across studies, although mean correlations were over 0.60. Some studies did not include numerical information, and some did not include enough descriptive information. However, compared with

Table 4
Convergent validity in felid personality assessment.

Dimension study	Trait	Criterion measure		Validity coefficient	95% CI	Sample size
		Type of test	Basis for scoring			
Active						
Gartner and Powell (2012)	Active/Vigilant	Novel object test	Number of visits to object	0.74		11
			Time spent locomoting	0.75		
			Time spent exploring	0.75		
Phillips and Peck (2007)	External awareness		Number of approaches by keepers	0.86		7
Wedl et al. (2011)	Active	Behavioral observations	Non-overlapping patterns	0.91		40
			Non-overlapping patterns per minute	0.93		40
			Event type complexity	0.93		40
Wielebnowski (1999)	Active	Novel object test (mirrors)	Number of approaches	0.55		44
			Sniff	0.35		
			Stare	0.35		
			Growl/Hiss	0.61		
			Approach time	−0.25		
Wielebnowski et al. (2002)	Pace	Fecal corticoid concentrations		0.35		72
Unweighted mean				0.72	0.49, 0.79	
Sample-weighted mean				0.57		
Aggressive						
Feaver et al. (1986)	Aggressive	Behavioral observations	Stare + Hit + Chase	0.85		14
Wielebnowski (1999)	Aggressive to conspecifics	Novel object test	Growl/Hiss	0.59		44
	Aggressive to people		Number of approaches	0.45		
			Stare	0.32		
			Growl/Hiss	0.44		
Unweighted mean				0.57	0.28, 0.78	
Sample-weighted mean				0.48		
Calm						
Wielebnowski (1999)	Calm	Novel object test	Stare	−0.38		44
			Growl/Hiss	−0.31		
			Approach time	−0.50		
Unweighted mean				0.40	0.16, 0.64	
Sample-weighted mean				0.40		
Curious						
Durr and Smith (1997)	Attention span	Behavioral observations	Latency of approach	0.76 (Group 1)		11
				0.88 (Group 2)		11
Feaver et al. (1986)	Playful	Behavioral observations	Play	0.60		14
Gartner and Powell (2012)	Curious/Playful	Novel object test	Number of visits to object	0.79		11
		Novel object test	Time spent locomoting	0.77		
		Novel object test	Time spent exploring	0.73		
Wielebnowski (1999)	Curious	Novel object test	Approach time	−0.62		44
Unweighted mean				0.75	0.65, 0.83	
Sample-weighted mean				0.70		
Dominant						
Durr and Smith (1997)	Dominant	Novel object test	Latency to approach	0.72 (group 1)		11
				0.90 (group 2)		11

Natoli et al. (2005)	Proactive	Social rank		0.71		14
		Social rank		0.67		10
		Social rank		0.77		21
		Reproductive success		−0.73		14
		Reproductive success		−0.68		21
van den Bos and de Cock Buning (1994)	Agonistic (offensive threats)	Behavioral observations	Rank	0.80		10
Unweighted mean				0.76	0.68, 0.81	
Sample-weighted mean				0.74		
Excitable						
Wielebnowski (1999)	Excitable	Novel object test	Number of approaches	0.35		44
			Approach time	0.33		
Unweighted mean				0.34	0.21, 0.47	
Sample-weighted mean				0.34		
Self Assured						
Wielebnowski (1999)	Self-assured	Novel object test	Approach time	−0.50		44
Shy						
Meier and Turner (1985)	Shy		Fleeing	0.38		26
Sociable						
Feaver et al. (1986)	Sociable with people	Behavioral observations	Approach + sniff + head and body rub observer	0.69		14
McCune (1995)	Friendly fathered (bold)	Familiar person test	Latency to 1 m	0.97		37
			Latency to 50 cm	0.97		37
			Latency to touch	0.95		37
			Latency to rub	0.95		37
			Number of rubs	0.86		37
			Total time <1 m	0.97		37
			Number of vocals	0.93		12
	Socialized		Latency to 1 m	0.95		37
			Latency to 50 cm	0.95		37
			Latency to touch	0.97		37
			Latency to rub	0.96		37
			Total time <1 m	0.95		37
			Number of vocals	0.95		12
	Friendly fathered (bold)	Stranger approach test	Latency to 1 m	0.97		37
			Latency to 50 cm	0.96		37
			Latency to touch	0.90		12
			Number of rubs	0.89		12
			Total time <1 m	0.96		37
	Socialized		Latency to 1 m	0.97		37
			Latency to 50 cm	0.94		37
			Latency to touch	0.96		12
			Latency to rub	0.94		12
			Number of rubs	0.90		12
			Total time <1 m	0.94		37
			Number of vocals	0.95		12

Table 4 (*Continued*)

Dimension study	Trait	Criterion measure		Validity coefficient	95% CI	Sample size
		Type of test	Basis for scoring			
	Friendly fathered (bold)	Novel box test	Latency to emergence	0.94		12
			Latency to 1 m	0.97		37
			Latency to 50 cm	0.95		12
			Latency to touch	0.98		12
			Number of times in box	0.97		12
			Part body in box	0.97		12
			Whole body in box	0.97		12
			Total time in box	0.90		12
			Total time <1 m	0.97		12
	Socialized	Novel box test	Latency to emergence	0.94		12
			Number of vocals	0.91		12
van den Bos and de Cock Buning (1994)	Affiliative	Behavioral observations	Rank	0.66		10
	Social licking	Behavioral observations	Rank	0.71		10
	Social rubbing	Behavioral observations	Rank	0.66		10
	Social sniffing	Behavioral observations	Rank	0.56		10
Wedl et al. (2011)	Sociable	Behavioral observations	Number of patterns	0.90		40
			Number of patterns per minute	0.90		40
			Non-overlapping patterns	0.96		40
			Non-overlapping patterns per minute	0.96		40
Unweighted mean				0.94	0.88, 0.94	
Sample-weighted mean				0.93		
Subordinate						
van den Bos and de Cock Buning (1994)	Agonistic (defensive threats)	Behavioral observations	Rank	−0.79		10
Timid/Fearful						
Wielebnowski (1999)	Fearful of conspecifics	Novel object test	Approach time	0.52		44
	Fearful of people	Novel object test	Stare	0.27		
	Fearful of people	Novel object test	Approach time	0.40		
Wielebnowski et al. (2002)	Tense	Fecal corticoid concentrations		0.33		72
	Hide	Fecal corticoid concentrations		0.25		
Unweighted mean				0.36	0.22, 0.49	
Sample-weighted mean				0.34		
Vocal						
Feaver et al. (1986)	Vocal	Behavioral observations	Chirp + cry + mew + hiss + growl	0.67		14
Voracious						
Feaver et al. (1986)	Voracious	Behavioral observations	Eat/drink	0.75		14

95% CI = 95% confidence interval.

similar reviews on dogs (~19%) (Jones and Gosling, 2005) and primates (~10%) (Freeman and Gosling, 2010), there is a reasonable amount of reliability statistics being reported in felid personality research. However, reliability should be a requisite for personality research, so the aim is to have all of the studies including this information. Most of the studies in this review measured inter-rater reliability. It would be useful for future studies to include this information, but also internal consistency (only two studies in this review did so), as well as test-retest reliability, to provide a better picture of how reliable each measure is within and across studies. Measures that were not used at all in these studies, but have been shown to be effective in primate studies (e.g., Weiss et al., 2006) include intraclass correlations (Shrout and Fleiss, 1979) for continuous measures and Cohen's kappa (Cohen, 1960) for categorical measures. It is clear from the results that personality studies in domestic cats need to report reliability and validity coefficients more consistently.

Convergent validity on some personality dimensions was strong. The dimensions with the highest validity for all species were Sociable, Dominant, and Curious. These were followed by Aggressive, Calm, Timid/Fearful, and Excitable. For wild cats alone, Curious had the highest validity, followed by Active/Vigilant, and Timid/Fearful, and for domestic cats Sociable did, followed by Curious and Dominant. There were seven dimensions only found in one study each. One each of these was found in two wild species—this may explain why they were not present in domestic cats or the other wild species. Two of the remaining five, "Rubbing" and "Feeding" were based more on single behaviors and therefore cats in other studies may not have had the opportunity to present this type of behavior, or alternatively, the authors of other papers may not have measured this type of behavior. Similarly, "Arrogant/Calculating," was only measured in one study—this study was the only one to utilize the Interpersonal Adjective Scales-Revised survey (Wiggins, 1995). The remaining two studies utilized a survey based on the Five-Factor Model (Digman, 1990) and therefore found "Conscientiousness," and "Intellect/Openness," which would not have been measured in other studies. These examples show the importance of measuring personality in a consistent way in order to compare results among studies.

Across some behavioral observations, novel object tests, and surveys, reasonable consistency has emerged for certain traits (although not all), and some personality dimensions seem to be consistent. However, because there are differences throughout the research in types of measurement and dimension names, there is no conclusive definition of cat personality established by these studies, nor is there one single method for assessing it that has proved to be reliably consistent.

In addition to the variety of methods used, there are also some limitations to the measures. Surveys are generally well-accepted and validated ways of assessing animal personality—indeed, more reliable than behavioral observations and less subjective than often assumed (Vazire et al., 2007)—as long as the people evaluating the animals have worked with the animals for a long enough period of time (Gosling, 2001). This does not represent a problem in studies of privately owned animals, then, but for those carried out in zoos, and especially free-ranging colonies and research facilities, how long a caretaker has spent with an animal should be noted. All the studies assessed here addressed this issue, although sometimes without stating actual amount of time spent with the animals.

Only four of the studies used behavioral observations as the only form of assessment. This type of method has the potential problem of assessing behaviors taken out of context (Vazire et al., 2007), so amount of time spent carrying out the observations—and consistency of when and where the observations are carried out—is important. This was addressed in the studies assessed in this review by retesting over years, or long hours of observations—none less than 3 months. Another potential problem with behavioral observations is the effect the researcher may have on the animal. This is rarely addressed in personality studies, and should be assessed for its possible impact on results.

The convergent validity of personality may be an artifact arising from the fact that, in many studies, the person rating the animal is the same one conducting behavioral observations. However, findings that validation across methods works well regardless of whether the person doing the rating is the same person doing the observing (e.g., in deer, Bergvall et al., 2011), indicate that this is unlikely. Still, it is important that studies show inter-observer agreement, and, where possible, use independent observers and raters.

One problem that often occurs in nonhuman animal studies for practical reasons is small sample size. The largest sample size among these studies was 440 (an outlier: the next largest was 196, then 106), the smallest 7 (mean $n = 63.2$, $SD = 98.70$). However, if this is taken into account while designing statistical analysis, problems should be minimized. Nevertheless, it may be hard to generalize out to the species level, for example, especially when demographic information (all one gender in a particular study, for example) is inconsistent.

There is evidence of age effects on some animal personality dimensions (e.g., Weiss et al., 2007), and that personality traits may be plastic (e.g., Frost et al., 2007). Most of the domestic cat studies focused on young animals, so future studies should include a wider range of ages or longitudinal designs to see how age may affect personality. These results may influence how we characterize personality in different species—for instance, animals with longer maternal care may show differing effects on personality than those without.

Breed was rarely included or noted in the domestic cat studies. Since there has been some work suggesting behavioral differences between pure-bred and non-pedigree cats (Turner, 2000), and dogs (Duffy et al., 2008; Svartberg and Forkman, 2002) this information should be included in personality studies. Another aspect of domestic cat variability was whether the cat was neutered or spayed. There is no research that looks at the differences in personality in cats that are intact versus those that are neutered or spayed, so this is a possible confound that should be addressed, as it does seem to play a role in other species, like dogs (Maejima et al., 2007).

Despite this variability, the studies do seem to be measuring personality, however, or some aspect of it. By using either multiple methods that were correlated, surveys that aggregate knowledge of time and context, or test-retest reliability, the studies avoided measurements at one point in time, or during only one context. Therefore, comparisons among the studies, as shown by the relatively high levels of correlation, can be considered valid, although it would be preferable to have a consistent method of measure across a number of studies with a variety of contexts to more definitively say that these constructs are describing cat personality.

It is obvious from this review that much more work on personality needs to be done in wild cats. Felid personality research has focused on a very small percentage of total species (~14%), with a large majority focusing on domestic cats (~85%). With only four personality studies on wild cat species, it is hard to draw any conclusions.

6. Implications

The study of personality can have far-reaching effects for cat species, including aiding in conservation efforts and captive animal management, and improving well-being and welfare. Few studies have addressed these issues, but the ones that have show promising results.

6.1. Conservation

Personality has been used in conjunction with other conservation methods, to better assess an animal's readiness for reintroduction. Bremner-Harrison et al. (2004) found that cautious swift foxes (*Vulpes velox*) were more successful in release scenarios than bold ones. Foxes that died within 6 months of release were all described as bold. Foxes assessed as bold by novel object tests were shown to travel further after release, and the authors suggested that they were less likely to avoid predators, conspecifics, or other potential risks.

Understanding personality has also been shown to have an effect on captive breeding, including choosing optimal breeding animals and pairing animals. Carlstead et al. (1999) found that the most successful breeding occurred when dominant female black rhinoceros (*Diceros bicornis*) were paired with submissive males, and that this was the most important behavioral predictor of successful breeding among the factors the authors assessed.

Similarly, Powell et al. (2008) found that high scores on shyness in female giant pandas (*Ailuropoda melanoleuca*) were correlated with poorer sociosexual performance, while bold, confident females were less likely to be aggressive to males, and more likely to show interest in them. The authors suggested that bold males may have increased sociosexual performance.

Wielebnowski (1999) also found that personality can play a role in captive breeding success. While female cheetahs scored higher on the dimension tense-fearful than males, non-breeding cheetahs of both sexes scored high on that dimension.

6.2. Animal management

Personality has applications for captive management in areas other than breeding (Watters and Powell, 2012). There is some evidence that personality may play a role in how animals are grouped (Barlow et al., 2006; Gold and Maple, 1994; Powell, 2010). For example, bachelor gorilla (*Gorilla beringei beringei*) groups formed with silverbacks that were two standard deviations above the mean for the personality factor Understanding (as described by Gold and Maple, 1994) were successfully maintained (Stoinski et al., 2004). In other cases, these types of groups are the most successful when the group is comprised only of young animals.

Because personality is associated with health outcomes (Deary et al., 2010), its use in captive situations could be vital. For example, it has been shown to interact with behavioral reactions to stress. Solitary, irritable, and aggressive Diana monkeys (*Cercopithecus diana*) demonstrated increased abnormal behavior during high visitor density, while active, playful, and excitable monkeys showed an increase in species-typical behaviors, including play (Barlow et al., 2006). In addition, Wielebnowski et al. (2002) found that clouded leopards (*N. nebulosa*) rated as more fearful/tense had increased overall, base, and peak fecal corticoid concentrations, indicating chronic stress. These results could be used to directly enhance the welfare of captive animals, for instance in choosing animals for exhibiting, or directed enrichment.

6.3. Health and well-being

Personality influences health outcomes other than stress, including morbidity and mortality (Deary et al., 2010). In humans and nonhuman primates, there is a relationship between immune response and personality, especially dimensions related to sociability, reactivity, and behavioral inhibition (Capitanio, 2011; Ironson et al., 2008). In addition, personality is one of the strongest and most consistent predictors of well-being in humans (Diener et al., 1999) and nonhuman primates (e.g., King and Landau, 2003). Recently, we found that this was also true for Scottish wildcats (*Felis silvestris grampia*), where well-being is positively correlated with Self Control (Gartner and Weiss, in press). There is also evidence that human well-being influences health (Diener and Chan, 2011). This also appears to be true for at least one species of nonhuman primate (Weiss et al., 2011). Thus, personality may be influencing health via subjective well-being.

6.4. Welfare

There is still little work done on the direct effect personality may have on captive animal welfare. Several researchers have made suggestions as to possible links, including the ideas that shy or fearful animals may need more places to hide (Gartner and Powell, 2012; Wielebnowski, 1999), or that an animal's physical behavior may need further explanation, which may lead to better understanding of welfare. For example, if a sheep is alert and active, is it also calm or is it fearful (Wemelsfelder,

2007)? How that animal is handled would be dependent on the latter assessment, and without knowledge of both the species and the individual, that animal's welfare could be impacted. For instance, in a study of farm pigs, veterinary inspectors were asked to score pig body language after observing the pigs for 10 min (Wemelsfelder, 2005). While the inspectors were used to rating pigs as healthy or unhealthy, the study offered them a tool to understand the "whole animal" (Wemelsfelder et al., 2001). That is, a physically healthy pig could nevertheless be frustrated or unhappy based on housing conditions. This, in turn, allowed the inspectors to discuss the situation with the farmers they were dealing with and to affect a change to improve the animal's welfare.

7. Conclusions

Felid personality dimensions with high validity for all species are Sociable, Dominant, and Curious. The methods used for studying personality—behavioral observations, novel object tests, surveys—are reasonably reliable, but more work needs to be done due to the variability of methods, small sample sizes, and singular context. Future studies need to include breed information, greater age range, and information on whether individuals were spayed or neutered. While the past three decades have seen an increase in the amount of felid personality research, much more work needs to be done, especially in wild species, where the practical applications of such work could have far-reaching effects for welfare, and ultimately, conservation.

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Scottish wildcat (*Felis silvestris grampia*) personality and subjective well-being: Implications for captive management

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ABSTRACT

Research in animal personality has been increasing over the last decade, as scientists realize its importance to health outcomes. In particular, personality has sometimes been used, in conjunction with other tools, for aspects of captive management, including decreasing stress, increasing positive health outcomes, successful breeding, and infant survival. A few such studies have focused on felids, and have shown that there are possible applications for personality in that taxon. This study looked at the Scottish wildcat (*Felis silvestris grampia*), a critically endangered species, with only an estimated 400 left in the wild. Raters assessed 25 Scottish wildcats on 42 traits and on a subjective well-being questionnaire. Mean inter-rater reliability on the personality items was 0.59 and 0.53 on the subjective well-being items. Three personality components were found using principal-components analysis: Dominance, Agreeableness, and Self Control. Higher Self Control was related to higher subjective well-being ($r = 0.67$, $P < 0.01$). Implications for the results of this and other similar studies are discussed.

1. Introduction

The study of animal personality has been increasing steadily since the last decade, and now is comprised of a wide number of species (fish, birds, primates, dogs, felids, and more—see Gosling, 2001, for an overview) with a diversity of goals (for example, reducing aggression, increasing welfare, understanding development, assessing methodological problems, and human–animal interactions). One application of personality research that is not widespread, however, is for captive management purposes. In conjunction with other tools and methods, however, personality seems to have the potential to address challenges often found in these types of situations (Watters and Powell, 2012), including captive breeding (Carlstead et al., 1999; Powell et al., 2008), enclosure grouping (Stoinski et al., 2004), well-being and welfare (Weiss et al., 2006; Wielebnowski, 1999), and overall health (Barlow et al., 2006).

While personality research is underused in captive management in general, it is extremely lacking in felid species. Of the 41 wild species of felids, 24 are endangered or in decline. But there are only three published studies on personality and wild cats. These studies, on snow leopards (*Panthera uncia*; Gartner and Powell, 2012), cheetahs (*Acinonyx jubatus*; Wielebnowski, 1999), and tigers (*Panthera tigris tigris*; Phillips and Peck, 2007), found similar and species-specific personality factors. Because felids, as wide-ranging, larger bodied carnivores, often face challenges in captivity, including increased stereotypies and infant mortality (Clubb and Mason, 2007), these results could have important implications for each species' management.

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A recent trend closely tied to animal personality research is the study of "subjective"[1] well-being in captive species. This area has its origins in research on humans that has shown that well-being is tied to personality and, in turn, is associated with positive life events (Lyubomirsky et al., 2005) and health (Diener and Chan, 2011). To date, studies of subjective well-being have primarily been conducted on humans and nonhuman primates, e.g. chimpanzees (*Pan troglodytes*; King and Landau, 2003).

This research in personality and subjective well-being shows that personality can play an important role in deciding how to handle captive animals. In addition, assessing more captive species is vital for the understanding, and successful handling, of each species. If an individual's personality can predict its well-being and health, then personality should be one of the tools that caretakers use for assessing the state of the captive animal.

Our study will thus examine both personality and subjective well-being in the critically endangered Scottish wildcat (*Felis silvestris grampia*). With an estimated 400 left in the wild, effective captive management for this species is crucial. Because they are closely related to the domestic cat (*Felis catus*), it is likely that their personality structure will be similar. Therefore, we expect to see three or four factors come out of the analysis, as has been found in domestic cats, such as Dominance, Neuroticism, or Extraversion (Gartner, unpublished study) or Alert, Sociable, or Equable (Feaver et al., 1986). Obtaining these measures for this species is an important step in addressing the challenges this species faces, both in captivity and in the wild.

2. Methods

2.1. Subjects

Subjects included 25 Scottish wildcats from three zoos. The age of the subjects ranged from 1 to 15 years (mean = 3.67 ± 3.14 sd). There were eight wildcats (3 males; 5 females) at Port Lympne Wild Animal Park (PL), in Lympne, Kent, UK; nine wildcats (2 males; 5 females, 2 unknown) at the Highland Wildlife Park (HWP), Kincraig, Kingussie, UK; and eight wildcats (4 males; 4 females) at the British Wildlife Centre (BWC), in Lingfield, Surrey, UK. All the zoos involved and the University of Edinburgh gave ethical approval for this research.

2.2. Participants

Eight caretakers rated the wildcats on two surveys. Three caretakers at PL rated the 8 wildcats there; 3 caretakers at HWP rated the 9 wildcats there; and 2 caretakers at BWC rated the 8 wildcats there. The caretakers knew the wildcats on average for 2.34 years (PL: mean = 2.83 ± .56 sd; HWP: mean = 1.57 ± .60 sd; BWC: mean = 4.5 ± .3.54 sd).

2.3. Procedure

The personality survey was based on previous felid personality surveys (Feaver et al., 1986; Gartner and Powell, 2012; Wielebnowski, 1999), from which 20 traits were taken. Twenty-two traits from the Hominoid Personality Questionnaire[2] (Weiss et al., 2009) that could be associated with felid behavior and that might provide a better overall assessment of personality in conjunction with the other traits were also included. Any wording specified to primate behavior was replaced with that describing typical cat behavior (for example the section of the description of chimpanzee "fearful" that included the words screaming and grimacing was replaced with "retreats readily from other wildcats").

A list of 42 adjectives was given to caretakers to rate each wildcat in their care (see Supplementary material). Definitions for each trait were provided related to the behavior of the species, and the caretakers were instructed not to discuss their ratings with other caretakers. The traits were rated by caretakers on a seven-point Likert scale, where one, "not at all," meant the trait did not describe the animal at all, and seven "very much so," meant the trait described the animal to a great degree.

The four-item subjective well-being survey[2] was developed by King and Landau (2003) for chimpanzees. The first two items measured overall moods of the wildcats and whether social interactions were enjoyable as opposed to negative, respectively, and were meant to assess the balance of positive and negative affect. The third item measured personal control, and asked whether the wildcat was effective in achieving its goals. The last item asked how happy the rater would be to be the specific wildcat. These items were rated on a seven-point Likert scale, where one was "least" and seven was "most."

This survey was shown to be reliable in chimpanzees (King and Landau, 2003), orangutans (*Pongo pygmaeus* and *Pongo abelii*; Weiss et al., 2006), and rhesus macaques (*Macaca mulatta*; Weiss et al., 2011a,b). In each of these studies, the items were reduced to a single factor, labeled subjective well-being.

2.4. Analyses

Unless otherwise noted, analyses were carried out using IBM SPSS 19 for Macintosh. For both surveys, inter-rater reliabilities were calculated using the intraclass correlation coefficients ICC(3,1) (the reliability of individual ratings) and ICC(3,*k*) (the reliability of the mean ratings of *k* raters) (Shrout and Fleiss, 1979). Items that were not reliable, defined as having an ICC(3,1) and/or an ICC(3,*k*) less than or equal to zero were omitted from further analyses.

After identifying the reliable items on both scales, we obtained the means across raters for each item on each animal. We then, for each scale, subjected the items to principal-components analysis. The number of components to extract was determined via parallel analysis (Horn,

[1] The word subjective refers to the measurement of an animal's experience, including the balance of positive and negative affect, and the perceived amount of control over important events (King and Landau, 2003).

[2] Available at http://extras.springer.com/ using ISBN 978-1-4614-0175-9.

1965; O'Connor, 2000) and by examining the scree plot. For confirmation, because the sample size was small, we also conducted a regularized exploratory factor analysis (Jung and Lee, 2011; Jung and Takane, 2008). This method of factor extraction is designed for small sample sizes. Factor extraction was calculated with MATLAB 7.12.0.635 (R2011a), using a program provided by Sunho Jung. We derived factor loadings via unweighted least squares and assumed that unique variances did not differ across items. We rotated the components using the varimax procedure in R version 2.15.1 (R Core Team, 2012).

As in previous studies (e.g., Weiss et al., 2006; Konečná et al., 2012), we defined factor loadings $\geq|0.4|$ as salient for the principal-components analysis, and $\geq|0.3|$ for the regularized exploratory factor analysis, which yields more conservative loadings. Also as in previous studies, if an item had multiple salient loadings, we assigned that item to the component that had the highest loading. Based on these loadings, we created unit-weighted factor scores (Gorsuch, 1983), which we then transformed into *z*-scores.

3. Results

3.1. Inter-rater reliabilities of items

For the personality items, the reliabilities of individual ratings, ICC(3,1), ranged from 0.04 (*quitting*) to 0.75 (*aggressive to conspecifics*), with a mean reliability of 0.41. The reliabilities of mean ratings, ICC(3,*k*), ranged from 0.10 (*quitting*) to 0.89 (*aggressive to conspecifics*), with a mean reliability of 0.59.

For the subjective well-being items, the reliabilities of individual ratings, ICC(3,1), were 0.24 (be the cat), 0.39 (ability to achieve goals), 0.26 (pleasure from social interactions), and 0.32 (moods), with a mean reliability of 0.30. The reliabilities of mean ratings, ICC(3,*k*), were 0.45 (be the cat) to 0.63 (ability to achieve goals), 0.49 (pleasure from social interactions), and 0.55 (moods), with a mean reliability of 0.53.

3.2. Principal-components analysis

3.2.1. Personality

Parallel analysis and examination of the scree plot indicated that three components accounting for 54.29% of the variance were described by the ratings (Table 1). We compared the results of the principal-components analysis and the regularized exploratory factor analysis by calculating Tucker's congruence coefficients (Wrigley and Neuhaus, 1955): $r_c = 0.994$ for the first domain, $r_c = 0.993$ for the second, and $r_c = 0.990$ for the third. Values in the range of 0.85–0.94 reflect fair similarity, while those above 0.95 imply equality (Lorenzo-Seva and ten Berge, 2006).

Based on the pattern of component loadings and previous research on trait groupings, we labeled the three components we found for Scottish wildcats: Dominance, Agreeableness, and Self Control. The reliabilities of individual ratings, ICC(3,1), were 0.68 for Dominance, 0.74 for Agreeableness, and 0.40 for Self Control, with a mean reliability of 0.61. The reliabilities of mean ratings, ICC(3,*k*), were 0.85 for Dominance, 0.88 for Agreeableness, and 0.64 for Self Control, with a mean reliability of 0.79.

3.2.2. Subjective well-being

Parallel analysis indicated that one component accounting for 85.61% of the variance was described by the ratings. Three items had salient loadings (Table 2), so the fourth item (be the cat) was dropped from further analysis. The reliability of individual ratings, ICC(3,1), for subjective well-being was 0.32 and the reliability of mean ratings, ICC(3,*k*), was 0.55.

3.2.3. Correlation between personality and subjective well-being

Subjective well-being was positively correlated with Self Control in results from both the principal-components analysis ($r = 0.67$, $P = 0.001$) and the regularized exploratory factor analysis ($r = 0.45$, $P = 0.04$). Individually, Self Control was positively correlated with moods ($r = 0.61$, $P = 0.004$) and pleasure derived from social interactions ($r = 0.69$, $P = 0.001$) (Table 3). Individual results from the regularized exploratory factor analysis are reported in Table 3.

4. Discussion

Scottish wildcat personality and subjective well-being ratings were reliable across raters. The reliabilities of the dimensions were similar to those found in humans (McCrae and Costa, 1987; Pavot and Diener, 1993), chimpanzees (Weiss et al., 2009), orangutans (Weiss et al., 2006), and rhesus macaques (Weiss et al., 2011a,b).

Scottish wildcat personality ratings define three components. The first component, Dominance, had the highest loadings on the traits aggressive to people, dominant, and bullying; Agreeableness had the highest loadings on the traits cooperative, friendly to people, and trusting; and Self Control, which was related to higher subjective well-being, had the highest loadings on decisive, self-assured, and cool.

Scottish wildcat Dominance has some similarities to the cheetah dimensions Aggressive (aggressive to conspecifics and people) and Vocal-Excitable (active, excitable, eccentric[3]) (Wielebnowski, 1999). It was also similar to a snow leopard dimension labeled Active/Vigilant (active and vigilant) (Gartner and Powell, 2012).

Scottish wildcat Agreeableness was most similar to snow leopards, with elements of snow leopard Curious/Playful and Friendly to Humans, including all the traits—cooperative, friendly to people, trusting, curious and playful—but one (vocal). There was some similarity to tigers as well (Phillips and Peck, 2007), with the curious and playful elements of tiger Youthfulness.

Self Control had some similarities to cheetah and snow leopard factors (tense, not self assured or calm). The dimension had elements related to low and high Conscientiousness in humans (decisive, persevering/quitting, aimless, predictable) (Digman, 1990).

[3] Wielebnowski (1999) did not include this item within the definition of this personality dimension, as she defined salient loadings as $\geq|0.6|$ and the loading on this item was 0.51.

Table 1
Structure of mean trait ratings.

Item	Principal-components analysis			Regularized exploratory factor analysis		
	Dominance	Agreeableness	Self-Control	Dominance	Agreeableness	Self-Control
Aggressive to people	**0.88**	0.08	−0.05	**0.64**	0.11	0.14
Dominant	**0.87**	0.21	0.12	**0.64**	0.16	−0.01
Bullying	**0.83**	−0.19	0.30	**0.52**	−0.12	−0.04
Stingy	**0.82**	0.32	0.00	**0.54**	0.23	0.03
Excitable	**0.77**	0.18	−0.19	**0.45**	0.16	0.16
Aggressive to conspecifics	**0.74**	0.28	−0.35	**0.50**	**0.30**	0.28
Impulsive	**0.73**	−0.16	−0.31	**0.39**	0.00	**−0.30**
Jealous	**0.73**	−0.11	0.33	**0.48**	−0.10	−0.10
Constrained	**−0.72**	−0.03	−0.17	**−0.46**	−0.01	0.04
Eccentric	**0.72**	−0.15	0.11	**0.46**	−0.09	0.02
Affectionate	**−0.70**	0.32	0.31	**−0.41**	0.10	**0.33**
Deliberate	**0.56**	−0.17	0.34	−0.28	−0.10	−0.08
Active	**0.54**	0.01	0.36	**0.35**	−0.06	−0.17
Vigilant	**0.51**	0.06	**−0.50**	−0.24	0.15	**−0.34**
Stable	**−0.49**	0.07	0.14	**−0.32**	0.01	−0.14
Friendly to conspecifics	**−0.48**	0.32	0.25	0.26	0.10	−0.26
Independent	**0.41**	−0.19	−0.19	−0.21	−0.04	0.19
Cooperative	0.08	**0.81**	0.04	−0.04	**0.49**	−0.16
Fearful of people	0.15	**−0.79**	−0.24	−0.08	**−0.47**	**−0.32**
Friendly to people	−0.33	**0.76**	−0.02	0.22	**0.46**	−0.15
Trusting	−0.27	**0.74**	**0.41**	0.15	**0.40**	**0.44**
Curious	0.32	**0.71**	−0.12	−0.17	**0.44**	−0.02
Playful	0.03	**0.68**	**−0.50**	0.04	**0.47**	0.17
Suspicious	0.32	**−0.68**	−0.30	−0.18	**−0.36**	**−0.39**
Insecure	−0.07	**−0.67**	**−0.58**	0.10	−0.29	**−0.42**
Timid	−0.12	**−0.66**	**−0.57**	0.14	**−0.35**	**−0.45**
Vocal	−0.09	**0.52**	−0.27	0.10	**0.32**	0.07
Fearful of conspecifics	0.28	**−0.49**	−0.09	−0.16	−0.28	0.18
Decisive	0.27	−0.09	**0.82**	−0.22	−0.14	**0.37**
Tense	0.25	−0.38	**−0.78**	−0.07	−0.09	**−0.56**
Self assured	0.10	**0.43**	**0.60**	−0.11	0.16	**0.39**
Solitary	0.31	−0.37	**−0.60**	−0.11	−0.09	**−0.44**
Aimless	0.22	**0.43**	**−0.58**	−0.05	0.28	0.23
Quitting	−0.20	0.06	**−0.55**	0.13	0.10	0.21
Cool	−0.11	0.14	**0.55**	0.00	−0.01	**0.33**
Calm	−0.09	0.25	**0.52**	0.00	0.06	**0.30**
Persevering	0.36	−0.03	**0.49**	−0.21	−0.06	−0.18
Predictable	−0.09	−0.08	**0.46**	0.01	−0.10	−0.25
Anxious	−0.23	−0.34	−0.09	0.16	−0.18	0.10
Erratic	0.37	−0.36	−0.29	−0.14	−0.12	0.22
Smart	0.36	0.21	0.38	−0.18	0.07	−0.15
Submissive	−0.07	−0.21	0.01	0.04	−0.12	0.02

Note: Salient loadings are in boldface.

These similarities indicate possible parallels across felid species, which opens the door to the possibility of a taxa-level personality survey. This could provide some practical advantages in zoos, for instance increased sample sizes, decreased time commitment, and the facilitation of cross-species comparisons (Watters and Powell, 2012).

4.1. Applications of personality and well-being research

At the species level, understanding the nature of personality can have implications for captive management in several species. In addition to aiding in captive breeding, personality has been shown to play a role in grouping, well-being and welfare, and health in some species. It is therefore likely that personality could have similar implications in captive felids. There is no such work in Scottish wildcats, however, research in other felids and even other mammals, including humans, may offer clues as to how these relationships may occur in this species.

Table 2
Factor loadings of subjective well-being items.

Item	Loading
Estimate the pleasure derived from social interactions	0.909
Estimate the balance of positive and negative moods	0.915
Estimate the ability to achieve goals	0.828
Imagine how happy you would be if you were the wildcat	0.094

4.1.1. Captive breeding

Captive breeding has been shown to be influenced by personality in several species. Wielebnowski (1999) found that cheetahs (which evolved separately from *Panthera*, along with wildcats and other species) rated as Tense-Fearful were more likely to be non-breeders. She suggested that cheetah enclosures should be altered, for example, by providing more seclusion and numerous hiding places to decrease stress. Both Powell et al. (2008 in pandas *Ailuropoda melanoleuca*) and Carlstead et al. (1999

Table 3
Personality components and subjective well-being correlations (Spearman's rho).

Subjective well-being	Factor (PCA)			Factor (REFA)		
	Dominance	Agreeableness	Self-Control	Dominance	Agreeableness	Self-Control
Overall	0.027	0.114	0.674*	0.097	−0.104	0.452**
Moods	0.108	0.236	0.605*	0.145	0.031	0.434**
Goals	0.289	−0.278	0.341	0.317	−0.450**	0.003
Pleasure from social interaction	−0.185	0.119	0.689*	−0.087	−0.077	0.553*
Be the cat	−0.399	0.369	0.076	−0.495**	0.446**	0.322

* Significant at the 0.01 level.
** Significant at the 0.05 level.

in black rhinoceros *Diceros bicornis*) also found relationships between captive breeding and personality. These results suggest that breeding success may also be influenced by personality in Scottish wildcats—as a critically endangered species, this information may be vital to preserving the species, and research to determine such a link would represent an important next step.

4.1.2. Enclosure grouping

Because some cat species are believed to be semi-solitary (Kitchener, 2000), it makes sense that personality may influence how animals interact in a captive environment. Captive felids are often kept in multi-animal enclosures, and there is some evidence that social interaction may decrease abnormal behaviors and increase natural behaviors in pair-grouped captive tigers, for example (De Rouck et al., 2005). If this is the case, it seems likely that Scottish wildcats rated high on Agreeableness might fare better in group enclosures. Similarly, Stoinski et al. (2004) give the example of two groups of gorillas (*Gorilla beringei beringei*) including more than one adult silverback that were successfully formed possibly because each of the silverbacks had scored over two standard deviations above the mean for the personality factor Understanding (as described by Gold and Maple, 1994).

4.1.3. Personality, subjective well-being, and health

Subjective well-being has not been measured in cat species until now. However, there is a similar relationship between Scottish wildcat personality and subjective well-being to that in chimpanzees: King and Landau (2003) also found that subjective well-being was positively associated with Dependability, a dimension later labeled Conscientiousness, which bears similarities to Scottish wildcat Self Control. In fact, personality is one of the strongest and most consistent predictors of well-being in humans (Diener et al., 1999) and nonhuman primates (e.g. King and Landau, 2003). This is important because subjective well-being is associated with longer life in humans (Diener and Chan, 2011) and orangutans (Weiss et al., 2011a). As such, subjective well-being may be a good marker for health outcomes.

Some studies have linked personality and health outcomes in felids. Wielebnowski et al. (2002) found that clouded leopards (*Neofelis nebulosa*) rated as more fearful/tense, and who self injured, paced, slept, and hid more often, had increased overall, base, and peak fecal corticoid concentrations, indicating chronic stress. In addition, bold male domestic cats, while more successful at reproduction, are also more likely to contract feline immunodeficiency virus (FIV), a lethal disease (Natoli et al., 2005). There is evidence that personality is associated with health outcomes in humans (Deary et al., 2010) and other primates (Capitanio et al., 1999, 2008; Barlow et al., 2006; Kaplan et al., 1991; Laudenslager et al., 1990).

According to Deary et al. (2010), there are four major applications of personality to health care and the improved well-being of humans: heightened surveillance for those with traits related to earlier mortality; the development of specific, individual intervention strategies; targeted drug treatments; and improved relationships between patients and health-care practitioners. These can be translated into care for captive animals. For instance, both Wielebnowski (1999) and Carlstead et al. (1999) suggested that a better relationship between an animal and its keeper should improve welfare. This relationship could affect the remaining applications. Once relationships between personality and mortality in felids are established, keepers could attend differently to felids with personality profiles related to risk, especially in terms of behavioral abnormalities. Similarly, individual interventions could be based on this increased awareness, and grouping, enrichment and medical interventions could all be tailored to certain personalities. While zoo animals are not typically given drug treatments that address issues related to prevention of stress or personality, this might be an area for further research.

Each of these areas contributes to the overall welfare of an animal, since each works to decrease specific causes of stress. While some have suggested that personality factors have implications for increasing welfare directly (for example, Wielebnowski, 1999), more work is needed. This should be an important next step in furthering the literature on personality and welfare.

4.2. Future research

Considering the possible implications—successful captive breeding and enclosure grouping, increased well-being and welfare, and links to health outcomes—there is room for more research on this and other felid species. Replicating these results in a larger sample would be beneficial, as the sample size for this study was small. In addition, developing personality surveys directly or augmenting questionnaires such as the present one with items developed for each species studied and related species would help ensure that any traits specific to a species such as

the Scottish wildcat would not be missed (Uher, 2008). However, the benefit to using one cross-species survey is that species personality can then be compared directly (Weiss et al., 2011b). One way to combine the two methods would be to add behavioral observations of the species, and assess whether there are correlations between specific species behavior and overall personality traits.

5. Conclusions

Scottish wildcat personality and subjective well-being can be reliably rated by keepers at zoos. Three domains of personality were found in the species: Dominance, Agreeableness, and Self Control. Higher subjective well-being is associated with the high end of the personality dimension Self Control. With implications for captive breeding, well-being and health, these measures have the potential to increase the overall welfare of captive felids. It is clear from the field that there needs to be more research into felid personality, and, importantly, more of the research needs to be applied—that is, personality should be considered as a moderator when measuring the effectiveness of a variety of interventions in the captive situation.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.applanim.2012.11.002.

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Chapter 8
Applications of Personality to the Management and Conservation of Nonhuman Animals

David M. Powell and Marieke Cassia Gartner

8.1 Introduction

A growing body of literature over the last two and a half decades has shown us that, like humans, nonhuman animals demonstrate consistent behavioral differences from one another and sometimes from one population to another. These differences have been termed personality (e.g., Gosling and John 1999), temperament (e.g., Hansen and Møller 2001), and behavioral syndromes and types (e.g., Sih et al. 2004). These concepts have come from a variety of disciplines, including comparative psychology, behavioral ecology, evolutionary biology, ethology, and population genetics. Although people who work with animals regularly have known for some time that animals demonstrate these consistent behavioral traits, it has not been until recently that scientists have formally recognized the phenomenon in animals and actively engaged in research in this area. What were historically considered curious differences between individuals and populations are now thought to be of major significance in understanding how animals make decisions, how they interact with individuals of their own and other species, and how their populations evolve. It has also been suggested that these differences have or will have an influence on the persistence of populations in the face of anthropogenic environmental change (e.g., McDougall et al. 2006) and the likelihood that populations of some species can be reestablished in the wild (e.g., Bremner-Harrison et al. 2004).

We are still only beginning to understand (1) the extent of variation in individual differences in behavior within and between species; (2) the methods by which this variation can be measured; (3) the impact that this variation has on individual survival, reproductive success, and well-being; and (4) the impact that this variation

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has on the evolution of populations. In this chapter, we survey the theories, methods, and findings from personality research in nonhuman animals and discuss some of its current applications in management and conservation settings. Finally, we suggest some areas for future research and speculate on how personality could be more broadly utilized in the management of captive and free-ranging wildlife.

8.2 Personality in Nonhuman Animals

Although the scientific study of personality in animals is relatively new (Gosling and John 1999), it has engendered a large body of literature. Studied species include water striders (*Aquarius remigis*) (Sih and Watters 2005), three-spined stickleback (*Gasterosteus aculeatus*) (Bell 2005), felids [Wielebnowski 1999 for cheetahs (*Acinonyx jubatus*) and Wielebnowski et al. 2002 for clouded leopards (*Neofelis nebulosa*)], giant pandas (*Ailuropoda melanoleuca*) (Powell and Svoke 2008; Powell et al. 2008), orangutans (*Pongo pygmaeus/Pongo abelii*) (Weiss et al. 2006), chimpanzees (*Pan troglodytes*) (Weiss et al. 2007), gorillas (*Gorilla gorilla*) (Gold and Maple 1994), black rhinoceros (*Diceros bicornis*) (Carlstead et al. 1999a, b), rhesus monkeys (*Macaca mulatta*) (Stevenson-Hinde et al. 1980a, b), swift foxes (*Vulpes velox*) (Bremner-Harrison et al. 2004), and hyenas (*Crocuta crocuta*) (Gosling 1998), among others. Overwhelmingly, these studies have found that individual differences in behavioral tendencies or personalities do exist in nonhuman species (Gosling and John 1999).

The definitions of the terms used to describe these tendencies vary. The term personality is almost always used in reference to humans, and some argue that it should also be used for nonhuman animals (Gosling 2008). Temperament, although often used synonymously with personality, has also been defined as mainly having a genetic basis (Box 1999). A behavioral syndrome – a suite of correlated behavioral traits (Sih et al. 2004) – is defined on the species or population level. For example, one population may be more aggressive than another: populations of funnel web spiders with low food availability evolved higher aggression levels across contexts than populations with abundant resources (Riechert 1993). Sih et al. (2004) also discuss behavioral types, which are reflected in the behavior of individuals (a more aggressive animal versus a less aggressive one). Although the wording of definitions for temperament or personality varies from scientist to scientist, these terms are generally described as consistent behavioral differences in individuals over time and across contexts. It seems to us much more useful to think of them as consistent behavioral tendencies because personality characteristics likely exist along a continuum rather than in absolute dichotomous states (see discussion by Gosling and John 1999). Despite the varying terminology and definitions used, it is clear that these behavioral tendencies are real and are quantifiable in a variety of experimental and observational settings. In addition, hypotheses and predictions can be tested regarding the impact of personality on behavior, reproduction, survival, and well-being. In this chapter, we use the term personality for the sake of consistency.

8.2.1 Assessing and Measuring Personality

Assessment of personality in animals has historically been carried out in three ways: recorded behavior, observer ratings, and behavioral tests (Manteca and Deag 1993) (see Chap. 5) (Fig. 8.1).

The three classes of methods have their own advantages and disadvantages. Recording behavior of an individual in its "home" environment and/or social group (e.g., Bard and Gardner 1996) arguably provides the most reliable and comprehensive picture of what its consistent behavioral tendencies are in a variety of settings. The difficulty emerges when trying then to understand which behaviors are the most important for distinguishing individuals or how to compile behaviors into some kind of composite score (Altman 1974). Also, these methods require significant amounts of time so the animal can be observed in a variety of situations and the behaviors observed can be considered reliable responses.

In response to some of these issues, many studies have made use of observer ratings, behavioral tests, and in several studies a combination of the two. An observer familiar with the individual(s) should theoretically be able to provide feedback on the personality of the animal(s) because they have spent considerable time with the animal already and have seen its responses to a variety of situations (Vazire et al.

Fig. 8.1 Common behavioral tests of personality in animals often involve exposing them to novel objects, mirrors, or other challenges designed to assess reactivity. (Photos: Jessie Cohen, Mehgan Murphy, Smithsonian's National Zoo)

2007). Their observations can be used much more quickly to produce a sketch of the animal's personality. The challenges in this class of methods have been to (1) validate that what the observer says really reflects behavioral differences among individuals and (2) design surveys that incorporate and define anthropocentric terms that can be clearly understood by respondents and applied to animals (e.g., What does "confidence" look like in a lion?). Several studies have been able to validate observer ratings in terms of their reflection of behavioral differences (Carlstead et al. 1999a, b; Wielebnowski 1999; Powell and Svoke 2008), but in some cases researchers have found a lack of concordance between some behavioral traits and a surveyed characteristic or that a surveyed characteristic does not apply to the studied species (Gartner and Powell, submitted; Phillips and Peck 2007).

Behavioral tests have a long history in the field of psychology (Archer 1973). These tests are relatively easy to conduct, and the testing methodology can usually be standardized across subjects, a factor that is not always possible or practical to achieve in recorded behavior studies. As these methods have been used for some time, there is also a large body of literature from which to draw guidance and an understanding of comparative aspects of animal personality. However, these tests arguably measure only a narrow selection of personality traits (e.g., "reactivity" or "fear"). By design, these tests measure how animals respond to environmental challenges that may be considered threatening, and in most cases they test single individuals, so they cannot tell us about personality traits that relate to relationships and interactions with conspecifics (e.g., "sociable" or "playful"). There is also still the question of what variables behavioral tests actually measure (e.g., latency to approach a novel object) and how to interpret the behaviors observed during the test (e.g., playing with a novel object versus sitting on or next to it) (Fig. 8.2).

We see several viable lines of future research regarding the methodology of studying animal personality. First, in studies of recorded behavior, how much observation is needed to provide a reliable snapshot of behavior, and can indices or

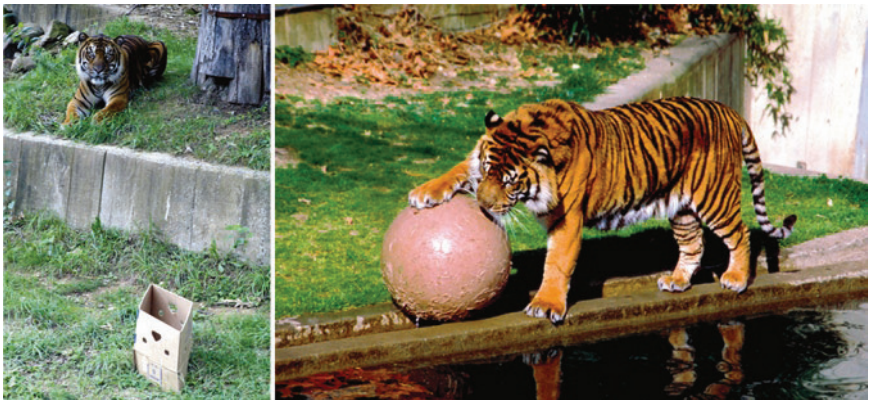

Fig. 8.2 Although novel object tests are a common tool for assessing animal temperament, it is not always clear what behavioral variables should be measured during the test and how they should be interpreted. (Photos: Jessie Cohen, Smithsonian's National Zoo)

composite scores be developed based on those observations that provide a holistic measure of personality? For observer rating studies, can a standardized set of personality traits or adjectives be identified and empirically defined that can be used across taxa or at least a subset of related species (e.g., felids)? This would significantly facilitate the comparison of findings across studies. Similarly for behavioral tests, is there a set of standardized variables to measure that are the most informative, and can we agree on their interpretation? Our review of the literature demonstrates that much of the animal personality work that has been done has focused on mammals, and it remains to be seen how well these methods of assessment work for other taxa.

8.2.2 Theoretical Treatment of Animal Personality

Until recently, the theoretical framework of personality was based largely on and applied to humans, without a corresponding body of personality theory for animals. Some psychologists are therefore looking into how transferable human theories of personality are to animals, and they are developing new theories that include nonhuman animals. Behavioral ecologists have taken theoretical and empirical approaches to understanding animal personality as well.

Gosling and John (1999) reviewed 19 studies of personality across 12 nonhuman species using the Five-Factor Model, a hierarchical model of personality that was developed from studies of humans and is one of the generally accepted theories of personality. Each of the five factors represents a broad, abstract level of personality, which is comprised of more specific traits, each of which can be described by certain behaviors. For instance, animals that are outgoing would be labeled social or active, and these traits would fall under the broad factor "extraversion versus introversion"; the four remaining factors are "neuroticism versus emotional stability," "agreeableness versus antagonism," "open versus closed to experience," and "conscientiousness versus carelessness." The authors found that three of these factors – extraversion versus introversion, neuroticism versus emotional stability, agreeableness versus antagonism – generalized the most across species. Open versus closed to experience followed, with seven of the species studied showing such traits. Finally, the factor labeled conscientiousness was found only in chimpanzees.

Recently, behavioral ecologists have developed a theory of personality around behavioral syndromes, or suites of correlated behaviors that are consistent across different contexts (Sih et al. 2004). It is posited that these syndromes can have both ecological and evolutionary implications (Sih et al. 2004). One aspect of the existence of behavioral syndromes is behavioral plasticity. If an individual with active tendencies always has active tendencies, a context that calls for cautiousness (e.g., a nearby predator) may not be met with the optimal behavior. Behavioral syndromes therefore explain "inappropriate" behaviors, but Sih et al. (2004) also argue that these syndromes are adaptive. In addition, behavioral syndromes can affect species distribution, tendencies of species to respond to environmental change, and speciation rates (Sih et al. 2004). For instance, activity syndromes can limit distribution in that very active animals typically stay in predator-free habitats,

whereas less active animals utilize predator-heavy habitats. Behavioral syndromes can affect a species' response to environmental change negatively: As mentioned earlier, the limited plasticity implied by the presence of a behavioral syndrome can lead to more predation but also to the decline of the species if too many "inappropriate" behaviors are exhibited, especially in a rapidly changing environment. However, if a mix of behavioral types is present among individuals, a species as a whole may be able to respond more appropriately because different survival strategies may then be exhibited. Finally, speciation rates are affected by behavioral syndromes in birds; for example, those that were more exploratory (specifically, showed more feeding innovations) had higher speciation rates (Webster and Lefebvre 2000 in Sih et al. 2004). According to Sih et al. (2004), the innovative behavior was socially transmitted and enabled the population to access new habitats, resulting in speciation.

Although personality is an individual attribute that likely has an effect on fitness (Biro and Stamps 2008) (see Chap. 6), the performance of individual behavioral types within a population depends partly on the mixture of behavioral types in that population because some behavioral types are more likely to cooperate with one another whereas others are more antagonistic. Researchers are just beginning to consider what impact personality has on overall group dynamics and the long-term stability and survival of groups. Sih and Watters (2005) found that the mixture of behavioral types in a group affects both individual and group fitness, which can depend on the social environment. By experimentally manipulating the behavioral types that comprised groups of water striders, the authors showed that the mix of behavioral types in the group affected the group outcome (e.g., a group of low activity/aggression males led to the creation of a hyperaggressive male, which inhibited mating in the group) and individual outcomes (the hyperaggressive males were less likely than the other males to mate).

8.3 Management and Conservation of Wildlife

Zoos and aquariums strive to maintain genetically and demographically healthy populations of animals for the long term. To this end, husbandry and management protocols are developed to keep individuals and populations physically and mentally healthy and capable of successful reproduction and rearing of offspring. The species in these settings have not evolved in the environments in which they now live, and they have not been subject to a long history of intense artificial selection for behavioral and/or physiological traits as is the case for domesticated animals. Working with comparatively small collections (as compared to laboratories and farms) of rare and endangered wildlife requires a keen ability to be able to predict how animals will cope with and respond to challenges from the physical and social environment. Because an animal's personality can predict how it will respond to different situations in which it is put, it can be used to understand and promote well-being (Vazire et al. 2007).

A central component of captive animal husbandry in zoos is environmental enrichment, which is the practice of providing stimulating environments for animals that

promote the expression of species-typical behavior and provide opportunities for animals to have choices and control over their environment (Association of Zoos and Aquariums Behavior Advisory Group 2009). Enrichment encompasses the design of appropriate exhibits, the management of species-typical social groups, and the introduction of stimuli (sights, sounds, smells, objects) to the animal's environment. Personality likely has a major influence on how animals respond to new environments (e.g., new exhibits or holding areas), to familiar and unfamiliar conspecifics and individuals of other species, and to changes in their surroundings. If the animal's personality, or the species' behavioral syndrome, is taken into account when designing environments and husbandry practices, well-being should be optimized.

Gartner and Powell (submitted) assessed personality in snow leopards (*Uncia uncia*) by examining their reaction to a novel object and comparing it to keeper assessments of personality via a survey. Their results suggested that personality could be used to design management programs, including assessing the value of enrichment and decreasing stereotypies; for instance, a shy animal should be given more places to hide, and a bold animal might need more novel items to explore.

Several authors have suggested that temperament be considered during the process of introducing animals to new exhibits and to each other (Gold and Maple 1994; Barlow et al. 2006; Powell 2010). For example, Gold and Maple (1994) identified four personality dimensions in captive gorillas and suggested that individuals with high scores on extroverted and low scores on dominant be used in the formation of bachelor groups (Fig. 8.3).

Scientists have also shown that personality plays a role in how captive animals react to zoo visitors. High densities of zoo visitors can cause stress for captive primates (Hosey 2000); however, other factors may come into play in regard to how animals react to visitors, and visitors may even act as enrichment in some cases (Hosey 2000). When captive Diana monkeys (*Cercopithecus diana*) were exposed to high visitor density, the personalities of various monkeys affected how they responded. Some individuals became more aggressive and exhibited abnormal behaviors, whereas others exhibited more affiliative behaviors (Barlow et al. 2006). Animals that were rated by observers as solitary, irritable, and aggressive demonstrated increased abnormal behavior when visitor density was high, whereas animals rated as active, playful, and excitable exhibited an increase in species-typical behaviors such as play. Thus, personality can be used to decide which animals go on exhibit during heavy visitor hours or during other potentially stressful events.

Personality has also been used to promote breeding success in endangered species that historically have had trouble breeding in captivity. Powell et al. (2008) studied personality in giant pandas using a novel-object test and correlated personality with sociosexual behavior. The authors found that high scores on shyness correlated with poor sociosexual performance. Based on that finding, the authors suggested that altering enclosures (providing environmental enrichment and more dens), increasing comfort levels with keepers, and reducing stress could improve reproductive success as these manipulations might reduce shyness (Fig. 8.4).

Fig. 8.3 Understanding animal personality and its behavioral manifestations are important in captive husbandry of wild animals – in this case understanding how lions respond to one another during an introduction. (Photos: Julie Larsen-Maher, Wildlife Conservation Society)

Fig. 8.4 Shyness correlates with poor sociosexual performance in giant pandas. Researchers suggest that improving relationships between giant pandas and their caretakers could reduce shyness. (Photos: Jessie Cohen, Mehgan Murphy, Smithsonian's National Zoo)

Wielebnowski (1999) suggested that assessing personality could allow predictions of reproductive success on an individual level. Using a mirror-image stimulation test and a keeper survey, she found three personality components in cheetahs: tense-fearful, vocal-excitable, and aggressive. Animals that did not breed successfully scored higher in tense-fearful than those that did breed, suggesting they had less ability to cope with the captive environment. The author suggested that the tense-fearful animals therefore may need more seclusion and more places to hide to breed successfully.

Carlstead et al. (1999a, b) found that the personality of the black rhinoceros included six components: olfactory behaviors; chasing/stereotypy/mouthing (a composite of aggressive and abnormal behaviors); fear; friendly to keeper; dominant (to conspecifics); and patrolling. Females that scored higher on dominant than the male they were paired with were more successful in breeding. Unsuccessful females also scored higher on chasing/stereotypy/mouthing, suggesting that either these females are incompatible with their mate or are behaviorally compromised by some other factor.

Personality may also play a role in parental care. Maestripieri (1993) found that individual differences influence maternal behavior in captive rhesus macaques. Using behavioral measures of anxiety (visual monitoring and scratching), he showed that visual monitoring of the infant and of other monkeys by the mother was correlated with maternal protectiveness and that the former was a better predictor of individual differences than age, experience, dominance rank, number of young in the group, or sex of the infant (Fig. 8.5).

These studies suggest that personality be formally added to the array of factors considered in the design of zoological facilities and husbandry protocols, particularly regarding species for which captive breeding is essential to their conservation. Breeding programs that make recommendations based on genetic compatibility should also consider compatibility in personality. Although more studies are needed, there is evidence that parental care is also influenced by personality; because captive maternal behavior is often problematic (Wielebnowski 1998), personality may be used to assess whether a problem is likely and then address it.

In addition to captive propagation, conservation plans frequently include reintroduction and/or translocation programs, which often are unsuccessful (Beck et al. 1994). Recent research suggests that personality could be a tool in planning such programs in addition to training animals that are to be released into the wild to cope with specific challenges that their new environment might present (McDougall et al. 2006). Personality has been shown to be a good predictor of survival in the wild, and it also can aid in handling animals before their release (e.g., Watters and Meehan 2007). Some studies have found that successful reintroduction programs can be informed by personality traits and suggest that although the use of this tool is not widespread it should be.

Bremner-Harrison et al. (2004) quantified the responses of 49 swift foxes to four novel stimuli and found two personality types: bold and cautious. They found that the swift foxes they had assessed as bold were not good candidates for reintroduction to the wild, as they had predicted they would be, as those animals died within 6 months

Fig. 8.5 Studies of nonhuman primates demonstrate that personality affects maternal behavior, specifically maternal protectiveness of infants. (Photo: Julie Larsen-Maher, Wildlife Conservation Society)

of reintroduction (two were killed by motor vehicles and the cause of death of the remaining animals classified as bold is unknown). Cautiousness was found to be more advantageous to fox survival in the wild. The authors concluded that this type of assessment is an important tool in predicting survival in released animals and should be used for animal selection and preparation.

However, Watters and Meehan (2007) argued that a one-size-fits-all theory of reintroduction may not always work and may be to blame for the high rates of failure associated with reintroduction of captive animals to the wild. Instead, the authors suggest that a range of personalities be introduced and monitored so it can become more apparent which personality types best equip a reintroduced animal to survive in a new environment. Those data can then be used for ongoing reintroduction programs and subsequent release.

For example, Sih and Watters (2005) assessed the personality of male water striders and then formed 12 groups based on the results: The most aggressive males were in one group, the next most aggressive in the next group, and so on until the last group, which was comprised of the least aggressive males. As discussed earlier, the authors found that the behavioral type of the group affected group outcomes.

The authors recommended that further studies be done on mixing behavioral types in groups to better understand the effects of such a mix on group outcomes.

The idea of a mix of behavioral types improving reintroduction success can also be applied before their release. Watters and Meehan (2007) argued that variation in behavioral types can be promoted by environmental factors, so attention to them before release may aid in successful reintroductions. The authors recommend that zoo managers provide different environmental contexts when rearing captive animals using environmental enrichment techniques, thereby promoting variation and developing a group more ready for reintroduction. In addition, they suggest that captive animals' personality be assessed and responses from each behavioral type to different environmental contexts be studied.

Other suggestions for establishing a community of animals in the wild include considering the family or neighborhood group as the reintroduction or translocation unit because such groups probably represent a compatible mix of personality types, which might influence their success, as Sih and Watters (2005) suggested. Shier (2006) found that prairie dogs that were translocated with their family groups intact were five times more likely to survive (predator success was decreased) and had better reproductive success than those that did not. It is possible that family groups that exhibit certain behavioral syndromes would fare even better, but that has yet to be studied.

Interestingly, group reintroduction is effective with typically solitary animals as well. Shier and Swaisgood (2009) found that Stephens' kangaroo rats (*Dipodomys stephensi*) that were translocated with neighbors fared better than those translocated with unfamiliar animals. The former did not travel as far from their release site and had higher rates of survival. Again, it is possible that certain personality types that are translocated with neighbor groups would fare even better, or that neighbor groups are successful because they contain a compatible mix of personality types. This should be studied to further the success of reintroduction programs.

8.4 Future Directions for Research and Application

Starting with the belief that only humans have personalities, to the acknowledgment that nonhuman animals do as well, to the use of personality as a conservation, management and well-being assessment tool – what more do we need to know and where can personality take us next? One important area of research is establishing an understanding of how much the physical and social environment affects personality and to what extent personality is plastic. Given that some individuals fare better in managed environments (e.g., zoos and reintroduction/translocation programs), can we somehow change those environments and associated protocols to improve how all of the individuals fare? Is it possible to produce more dominant female black rhinoceros and less shy giant pandas? We suggest that longitudinal studies of personality be carried out to assess how it may or may not change over time and what factors or events coincide with the changes. We also suggest that

researchers assess the impact of rearing environments (physical and social) on personality so even if personality is a life-long consistent trait we might have some ability to send individuals down differing developmental paths that culminate in different personalities (Fig. 8.6).

Similarly, groups of related and unrelated animals should be reared in standardized environments, and the heritability of personality traits should be measured to determine the extent of a genetic component to personality. More work should focus on the fitness or viability of populations that vary in regard to either dominant personality traits (e.g., a generally "bold" population) or in the composition of personality types (see reviews by Dingemanse and Réale 2005; Réale et al. 2007; Smith and Blumstein 2008). These basic studies would have obvious management and conservation applications.

In terms of captive animal well-being, might it be possible to further incorporate personality into veterinary care? Do different behavioral types respond differently to treatment? When immobilizing animals for treatment, veterinarians make every effort to keep the animals as calm as possible during the process so the anesthetic drugs have an optimal effect. In these situations, individual personality probably plays some role in keeping the animal calm before the anesthetic is administered. Might this also be true for therapeutic medications? In humans, studies have shown that some people who have a better outlook on life follow treatment plans better and demonstrate faster recovery times from some diseases (for depression, MacLeod and Moore 2000; for cancer, Greer et al. 1979; but see Wilkinson and Kitzinger 2000) – is there also a relation between personality and morbidity or mortality in zoo populations?

A common reason for mortality in reintroduced or translocated populations is dispersal from the reintroduction site (Fischer and Lindenmayer 2000). What is mediating this dispersal drive? Individuals might be dispersing in an attempt to find a familiar landscape (Stamps and Swaisgood 2007), because they cannot integrate into the resident population (Kleiman 1989), or it may simply be due to stress. It is possible that personality is a factor. Different types may be more or less able to find

Fig. 8.6 The extent to which the environment affects the development of personality is an avenue of future research that would be beneficial for the management and conservation of wild animals. (Photos: Jessie Cohen, Smithsonian's National Zoo)

resources (e.g., "curious" types), establish their own territories (e.g., "bold" individuals), form social relationships (e.g., "calm," "sociable" types), or cope with stress. It is likely that the "right" type of individual for reintroduction or translocation will vary by species and the ecological characteristics of the site, including the demographics and personality composition of the resident population, if one exists.

We are in the midst of an extinction crisis that is unprecedented in scale. The survival of many species depends on the extent to which they can endure anthropogenic environmental change and in some cases become commensal with humans (e.g., gray squirrels, *Sciurus carolinensis*; "temple monkeys," *Macaca* spp. and *Presbytis* spp.). It is possible that different personality types fare better than others in the face of these selective forces. Alternatively, the degree to which personality is plastic may be the deciding factor regarding whether a species or population adapts. It has also been suggested that personality plays a role in the likelihood that a species becomes invasive (Réale et al. 2007). For example, is it a bold type or behavioral syndrome that is more likely to invade owing to its aggressive nature, or would it be a cautious or timid type that would survive the hazards of the unknown environment? Is it possible that personality affects whether an individual becomes a nuisance or problem animal (e.g., man-eating large carnivores, crop-raiding animals, campsite-raiding bears)? If so, could we then attempt to shape personalities away from those tendencies, or could we identify these "problem types" in advance and proactively relocate or control them some other way?

8.5 Conclusion

The concept of personality in animals is maturing as we continue to document the diversity of personality types and characteristics in different species and learn how to measure them. Theories from psychology and behavioral ecology are enriching our understanding of animal personality and are allowing us to make predictions about the impact it has on behavior and evolution. The knowledge we have gained on animal personality has already begun to be put to good use in the management of captive animals, but there is significant room for more application. Animal personality has rarely been considered in conservation and wildlife management. We hope that our discussion here stimulates more theoretical and empirical work and expands the application of our current knowledge of animal personality to finding ways to conserve and live harmoniously with nonhuman species.

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Extraversion predicts longer survival in gorillas: an 18-year longitudinal study

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Extraversion predicts longer survival in gorillas: an 18-year longitudinal study

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Personality plays an important role in determining human health and risk of earlier death. However, the mechanisms underlying those associations remain unknown. We moved away from testing hypotheses rooted in the activities of modern humans, by testing whether these associations are ancestral and one side of a trade-off between fitness costs and benefits. We examined personality predictors of survival in 283 captive western lowland gorillas (*Gorilla gorilla gorilla*) followed for 18 years. We found that of four gorilla personality dimensions—dominance, extraversion, neuroticism and agreeableness—extraversion was associated with longer survival. This effect could not be explained by demographic information or husbandry practices. These findings suggest that understanding how extraversion and other personality domains influence longevity requires investigating the evolutionary bases of this association in nonhuman primates and other species.

1. Introduction

A large body of literature indicates that who we are or our 'character' has major consequences related to our health [1]. Most strikingly, studies indicate that lower levels of neuroticism and higher levels of conscientiousness, agreeableness, openness to experience and aspects of extraversion linked to positive affect, and activity are related to reduced risk of all-cause mortality [1,2].

Humans are not the only primate species for which personality is a determinant of health. For example, studies of rhesus macaques found that 'nervous temperament' was associated with more neutrophils, lymphocytes and both $CD4^+$ and $CD8^+$ T cells [3], and that sociability was associated with better immune response directly or by moderating the effects of stressful situations [4]. These and similar studies suggest that insights into personality evolution can be gained from studying personality and health outcomes in closely related species [5]. To these ends, we examined personality and longevity in western lowland gorillas (*Gorilla gorilla gorilla*).

Western lowland gorillas, henceforth gorillas, and humans shared a common ancestor approximately 10 Ma. Sequencing demonstrated that for approximately 30 per cent of the genome, gorillas are closer to humans or chimpanzees than the latter two species are to each other [6]. This phylogenetic proximity is reflected in gorilla personalities, which resemble those of their hominid cousins. Gorilla personality includes reliable, validated dimensions labelled dominant, extroverted, fearful, and understanding [7,8]. The first is not a measure of rank, but resembles dimensions associated with competitive prowess and labelled dominance or confidence in other primates [9]. The latter three resemble dimensions labelled extraversion, neuroticism, and agreeableness, respectively, in humans, chimpanzees and orangutans [10–12].[1]

We predicted that gorillas lower in neuroticism and higher in extraversion and agreeableness would live longer. Should this be the case, the most parsimonious explanation would be that associations between these personality

Table 1. Nested comparisons of accelerated failure time models to test for interaction effects. ($n = 283$. −2LL, −2 log likelihood of model; χ^2, model chi-square; d.f., model degrees of freedom; $\Delta\chi^2$ and Δd.f., chi-square and degrees of freedom difference between the baseline and comparison models; *p*-value, significance of $\Delta\chi^2$ with Δd.f; AIC, Akaike's information criterion.)

model	−2LL	χ^2	d.f.	$\Delta\chi^2$	Δd.f.	*p*-value	AIC
baseline	2418.2	65.78	10				2438.2
add sex × personality	2413.8	70.22	14	4.44	4	0.350	2441.8
add age × personality	2415.6	68.36	14	2.58	4	0.630	2443.6
add background × personality	2413.6	70.38	18	4.60	8	0.799	2449.6
add transfers × personality	2415.0	69.05	18	3.27	8	0.916	2451.0

dimensions and mortality in humans were present in the common ancestor of gorillas and humans. Moreover, based on a review of primate social hierarchies and health, we predicted that gorillas lower in dominance will experience more stress and, consequently, have poorer health [13]. In addition, we tested for interactions of personality and other potential predictors of mortality. For example, given the influence of social instability on rhesus personality and immune functioning [3,4], we tested whether there was an interaction between personality and the number of transfers between facilities an individual experienced.

2. Material and methods

(a) Subjects

We derived our sample from 298 gorillas whose personalities were rated in 1993 [7]. These gorillas represented over 98 per cent of gorillas in the North American Gorilla Species Survival Plan (SSP) over 1 year in age and lived in 43 North American institutions accredited by the Association of Zoos and Aquariums. For our study, we excluded 15 of these gorillas: eight had unknown rearing histories, one had missing personality data, five died from fire exposure, and one died from gas exposure.

At the time their personalities were rated, these gorillas (mean age = 16.5 years ± 10.8 s.d.) included 130 males (mean age = 14.4 years ± 10.1 s.d.) and 153 females (mean age = 18.4 years ± 11.1 s.d.) living in 42 institutions. Ninety-one subjects were wild-born; 82 were captive-born and parent-raised; and 110 were captive-born and hand-raised.

(b) Mortality surveillance

We used the Gorilla SSP studbook to gather data on survival time from 1 March 1993 through to 15 August 2011. If a gorilla died during this period, we coded their mortality status as 1 and defined survival as the number of days between 1 March 1993 and date of death. If a gorilla was still alive we coded their mortality status as 0 and survival time was defined as 6741, the number of days between 1 March 1993 and 15 August 2011 (the censoring date).

(c) Personality

Gorilla personality was assessed using the Gorilla Behavior Index (GBI; appendix B in [7]). The GBI includes 25 behavioural adjectives paired with brief descriptors, e.g. 'Active: moves about a lot.' Ratings were made on a 1 ('the item is weakly represented') to 5 ('the item is very strong and conspicuous, approaching the extreme') scale. We computed *z*-scores for the personality dimensions based on factor definitions from the previous study ([7]; table 1). For a more detailed description of the rating procedure, see the electronic supplementary material.

(d) Covariates

Because sex and age effects on personality have been found in chimpanzees [14] and gorillas [8], respectively, we included these variables in our models. This ensured that any significant effects of personality could not be explained by their association with sex or age. To rule out confounds related to rearing, we included two sets of coded variables derived from information in the studbook. The first set included two dummy coded variables. One captive-born, mother-reared gorillas to wild-born gorillas. The other compared captive-born, hand-reared gorillas to wild-born gorillas. The second set included two dummy-coded variables indicating number of transfers (no transfers, 1 transfer, 2+ transfers) to new facilities before the personality ratings.

(e) Data analysis

We fitted six survival models using accelerated failure time analysis [15]. Based on preliminary analyses, we specified a Weibull distribution for survival time. Analyses were conducted using the `survreg` function in R [16]. In each model, predictors were entered simultaneously and thus were net of all other predictors. For ease of interpretation, associations between survival time and the predictors were expressed via the deceleration estimate ($\hat{c}$), which indicates the percentage difference in lifespan associated with a 1 unit change in the predictor. This estimate is computed by determining the antilog of the predictors' effects, i.e. raising the base of the natural log (e) to the power of a predictor's parameter estimates (b), and multiplying the value by 100.

The baseline model included sex, age in years at the time of the personality assessment, rearing type, birth type, number of transfers and the personality dimensions. This model was then compared with four models, each of which included four terms representing the interaction between one covariate and each of the four personality variables. The first tested for sex × personality interactions. The second tested for age × personality interactions. The third tested for rearing × personality interactions. The fourth tested for transfers × personality interactions. We compared models using difference χ^2 tests and Akaike's information criteria (AIC; [17]).

3. Results

Over the follow-up period, 119 subjects died. Days to death ranged from 93 to 6741 (median = 3923, mean = 3614.2 ± 1942.9 s.d.). Age at death ranged from 2.4 to 55.7 years

Table 2. Parameter estimates from the baseline model. ($n = 283$. $\hat{c}$, deceleration estimate; 95% CI, 95% confidence interval.)

	estimates			
parameter	*b*	s.e.	*p*-value	$\hat{c}$ (95% CI)
intercept	9.202	0.422	<0.001	
female sex	0.187	0.150	0.212	1.205 (0.899, 1.617)
age at personality rating	−0.024	0.015	0.103	0.976 (0.949, 1.005)
captive-born, mother-reared[a]	0.402	0.297	0.177	1.494 (0.834, 2.676)
captive-born, hand-reared[a]	0.412	0.246	0.094	1.510 (0.932, 2.447)
1 transfer[b]	0.154	0.221	0.486	1.166 (0.757, 1.797)
2+ transfers[b]	0.331	0.241	0.170	1.392 (0.867, 2.235)
extraversion	0.272	0.120	0.023	1.312 (1.038, 1.658)
dominance	−0.051	0.072	0.479	0.950 (0.826, 1.094)
neuroticism	0.108	0.072	0.134	1.114 (0.967, 1.283)
agreeableness	0.004	0.077	0.958	1.004 (0.864, 1.167)
log(scale)	−0.317	0.084	<0.001	

[a]Effect compared with being wild-born.
[b]Effect compared with never being transferred.

(mean = 31.7 ± 11.7 s.d.) and was normally distributed with half of the deaths occurring at 34.1 years or younger.

The baseline accelerated failure time model in which survival time was predicted by sex, age, background, number of transfers, and the four personality dimensions had the lowest AIC; none of the models that added interaction terms significantly improved model fit (table 1). The baseline model (table 2) indicated that females lived longer than males and that each year in age was associated with reduced survival time, though neither effect was significant. In this same model, being captive-born and mother-reared versus being wild-born was not related to survival time. There was also no significant effect of background; captive-born gorillas, whether mother- or hand-raised, did not differ in length of life from their wild-born counterparts. Compared with subjects that were not transferred, there was no significant effect of being transferred one time or being transferred two or more times. In terms of personality, only the effects of extraversion were significant, with each standard deviation being associated with just over a 30 per cent increase in lifespan (see figure 1).

We conducted two additional analyses. The first sought to determine whether the extraversion effects were influenced by a higher mortality rate in infancy and was based on 179 subjects that were at least 10 years old at the time of the initial assessment. The effect of extraversion in this subsample was significant ($\hat{c} = 1.354$, 95% CI = 1.046, 1.754, $p = 0.022$). The second was conducted to determine whether the non-significant effects of age and number of transfers were attributable to the confounding of age and number of transfers, i.e. older animals would have been transferred more throughout their lives than younger animals. To do so, we fitted three additional models. The first only included sex and age as predictors. The second only included sex and number of transfers. The third only included sex, age, and number of transfers. The first model revealed that older animals had shorter survival times ($\hat{c} = 0.951$, 95% CI = 0.937, 0.965, $p < 0.001$). The second model revealed that, although subjects transferred one time did not have

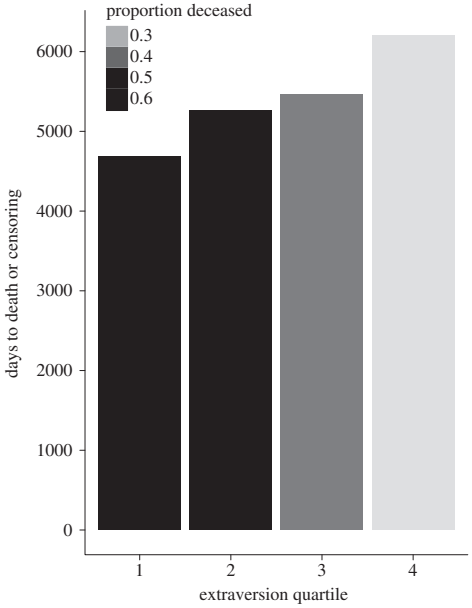

Figure 1. Unadjusted days to death or censoring for quartiles of extraversion ($n = 283$). Figure by the authors, licensed under a Creative Commons Attribution 3.0 Unported Licence and published under the terms of this licence. For more details see http://creativecommons.org/licenses/by/3.0/.

significantly different survival times than subjects who were never transferred ($\hat{c}_{1\text{ versus }0} = 0.699$, 95% CI = 0.468, 1.042, $p = 0.079$), subjects transferred two or more times lived just under half as long as those who were never transferred ($\hat{c}_{2+\text{ versus }0} = 0.511$, 95% CI = 0.352, 0.743, $p < 0.001$). The third model revealed that, after adjusting for age, the difference in survival time between individuals transferred once and those not transferred was not significant

($\hat{c}_{1\ \text{versus}\ 0} = 1.090$, 95% CI = 0.727, 1.632, $p = 0.677$). The same was true for the difference between subjects that were transferred two or more times and those who were not transferred ($\hat{c}_{2+8\ \text{versus}\ 0} = 1.167$, 95% CI = 0.770, 1.769, $p < 0.466$). Thus, the absence of significant age and transfer effects in our model are probably explained by these effects being confounded by other predictors, including personality.

4. Discussion

More extraverted gorillas lived longer than their more introverted peers; this association was not confounded by age or sex, rearing condition, or how many times the gorilla was transferred. This finding also did not reflect infant mortality or the deaths of very young gorillas. This finding is consistent with human studies [1,2] and suggests that the association between extraversion and longevity may have been present in the common ancestor shared by humans and gorillas. We would thus expect to find similar associations between extraversion and longevity in chimpanzees and bonobos who share this common ancestor [6].

These results suggest several causal mechanisms. First, like rhesus macaque sociability [4], gorilla extraversion could be a biomarker for differences in the functioning of the immune system. Second, gorilla extraversion could be related to stronger social ties and support that, as in humans, buffer individuals from the effects of environmental stressors [18]. Evidence consistent with this includes a study that showed an association between extraversion and higher rates of affiliation in a subsample of these gorillas [8]. Another possibility is that low extraversion could be linked to cardiovascular disease, which is the primary cause of mortality in captive gorillas [19].

Our other predictions were not supported. Neuroticism and agreeableness were not associated with survival. One possible explanation is that the association between these two personality dimensions and mortality emerged before the homo–pan split, approximately 2–4 Myr later [6,20]. If so, we would expect that neuroticism and agreeableness would be associated with chimpanzee and bonobo longevity. Alternatively, these null results may be an artefact of captivity as regular veterinary care, adequate nutrition, and lack of predation may buffer against untoward effects of higher neuroticism and lower agreeableness. Finally, these non-significant results may be attributable to gorilla social structure. Adult lowland gorillas typically live in cohesive single-male groups [21]. On the other hand, chimpanzees, bonobos and humans live in large multi-male–multi-female groups characterized by fission–fusion dynamics [22]. In the latter type of social groups, increased aggression associated with lower agreeableness [23] may lead to more frequent conflict with other group members and, hence, higher stress levels and hypothalamic-pituitary-adrenal axis activation. Similarly, living in large, complex and ever changing groups may lead to mortality differentials between individuals who differ in their susceptibility to stress. If differences in social structure were responsible, we would expect to find associations between these personality dimensions and longevity in chimpanzees, who live in large complex groups ([24]; but see [21]), but not in orangutans, a semisolitary species [25].

Contrary to our prediction, dominance was not associated with longevity. One possible explanation is that the zoo environment mitigated the effects of low dominance. For example, among wild gorillas, male and female dominance are related to competing over mates and food, respectively. As both are probably reduced or eliminated in captive environments, the consequences of related behaviours or physiological responses may be reduced. If so, we would expect to find a positive association between dominance and survival time among wild gorillas.

One limitation of the study was that data on cause of death, health outcomes and blood chemistry were unavailable. We were thus limited in our ability to understand the route by which extraversion led to longer life. Future researchers should attempt to replicate these findings and, together with zoological parks, collect these data for new studies on personality and health in gorillas and the other great apes.

Another limitation is that we cannot conclusively rule out the possibility that the association between extraversion and longevity may be confounded by characteristics of the gorillas' enclosures or social groups. For example, it may be that gorillas who were housed in small social groups appeared to be lower in extraversion and that these small social groups led to poorer health. To examine the possibility of confounding by zoo characteristics, we conducted two supplementary analyses. First, we tested whether social group size was a potential confound. This involved fitting a model identical to the baseline model, but including the number of subjects with personality data in each zoo as a proxy for social group size. The effects of extraversion held ($\hat{c} = 1.318$, 95% CI = 1.042, 1.667, $p = 0.021$). Second, we tested for the possibility of any other potential confounds related to the zoo environment or animal husbandry. Like the previous supplementary analysis, this involved fitting a model identical to the baseline model, but including the zoological park identity as a categorical variable. In short, we statistically adjusted for any differences across zoological parks in the housing and husbandry of the gorillas. The effects of extraversion in this model also held, and were somewhat stronger ($\hat{c} = 1.558$, 95% CI = 1.188, 2.043, $p = 0.001$). Thus, it is unlikely that the effects of extraversion were confounded by zoo level differences in housing and husbandry. In fact, differences among zoological parks seem to have 'masked' the effects of personality. Still, future researchers could learn much about this association by examining the degree to which these this association can be explained by specific differences in husbandry procedures, social group composition, physical environments, and enrichment.

This study revealed that the association between dispositions related to sociability, activity, and positive affect with longevity may have evolved at least 10 Ma. In doing so, it highlights ancestral fitness benefits of personality traits that might explain what kind of selection pressures maintain personality variability in humans [26] and our gorilla cousins. These findings also highlight how understanding the natural history of personality is vital to insuring the continued health and well-being of gorillas and other great apes, including ourselves.

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Endnote

[1]For consistency, we adopted labels used in previous studies.

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